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REVIEWS

Sociable schedules: interplay between avian seasonal and social behaviour

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Timing is essential in seasonally changing habitats. Survival and reproduction are enhanced through precise adjustment to environmental conditions. Avian seasonal behaviour, that is, diverse activities associated with reproduction, moult and migration, has an endogenous basis and is ultimately linked to changes in environmental factors such as food supply. However, behaviour occurs in social contexts, and interactions with conspecifics are intimately linked to seasonal activities. Time programmes set the stage for social behaviour, which in turn fine-tunes seasonal activities. We propose that avian schedules are genuinely 'sociable': birds communicate seasonal behaviour by both intentional and inadvertent information transfer and negotiate it in competitive and cooperative interactions. Studying the interplay between seasonal and social behaviour can add to our understanding of animal behaviour, including mechanisms by which birds could cope with changing environmental conditions.

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Birds can undertake spectacular seasonal journeys; for example, Arctic terns, *Sterna paradisaea*, almost circle the globe each year (Alerstam 1990; Berthold 2001). Migrations can be successful only if they coincide precisely with favourable conditions, not only at target locations but also at staging areas en route. Mistimed migration imposes high survival and fitness costs, such as when birds encounter severe weather conditions (e.g. James 1956; Brown & Brown 2000) or find reduced food resources at staging sites (Moore et al. 1995; Baker et al. 2003). The temporal precision of migratory birds has encouraged studies of their timing skills for almost a millennium (Gwinner & Helm 2003).

The need for accurate timing is not confined to migrants, however. Residents, such as great tits, *Parus*

major, and blue tits, *Cyanistes caeruleus*, time their clutches precisely to capitalize on the narrow peak in the availability of their primary nestling food, caterpillars (e.g. Perrins 1970; Visser et al. 1998). Even slight mismatches between breeding and food peak can impose measurable costs: spring weather changes have unsettled the phase relation between predictive daylength information and food peak, thus imposing energetic and fitness costs on tits (Visser et al. 1998; Thomas et al. 2001). Although less extensively studied, other annual events, notably moult, often also occur at precise times (e.g. Newton 1966; Stresemann & Stresemann 1967; Hahn et al. 1992; Jenni & Winkler 1994; Siikamäki et al. 1994; Nilsson & Svensson 1996).

Seasonal activities take place in social contexts, and social interactions are a crucial aspect of annual cycles. Avian social behaviour, defined as including all within-species interactions, rarely remains constant over time. Many species are solitary for part of the year, pair up for breeding and flock together for migration and wintering (Rappole 1995; Greenberg & Salewski 2005). Such transitions can be instantaneous: for example migratory species often claim territories and try to attract mates immediately upon arriving at the breeding grounds. Avian species differ widely in the plasticity and timing of their social

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behaviour. Reproductive 'partnerships' range from permanent mate attendance to breeding partners that reunite for only a few hours every year (Black 1996a, b). Similarly, territorial behaviour differs in timing and extent between species. Common stonechats, *Saxicola torquatus*, tolerate conspecifics during migration, but otherwise defend pair territories throughout the year (König et al. 2002; Urquhart 2002); more sociable species are territorial for only short periods of the year (e.g. red knots, *Calidris canutus*: Whitfield & Brade 1991). Highly social species, such as waterfowl, vigorously defend nest sites and feeding areas within a colony during the breeding season but may favour kin with which they associate in complex social interactions (Andersson & Åhlund 2000; van der Jeugd et al. 2002). The physiological basis for behavioural change is often endogenously programmed, as evidenced by annual fluctuations in seasonal activities and related key hormones (Gwinner 1986; Wingfield & Marler 1988). For example, aggression and plasma testosterone of young African stonechats held in Germany rose spontaneously when free-living conspecifics established territories (König et al. 2002).

In this paper we aim to integrate research on timing and social interactions. We first discuss timing mechanisms and social interactions from behavioural and evolutionary perspectives. We propose that avian schedules are genuinely 'sociable': seasonal activities are inadvertently and actively communicated and are often negotiated in conflict and cooperation. We illustrate the interplay between seasonal and social behaviour by selected examples throughout the annual cycle. A more detailed yet still incomplete review of literature is given in Table 1. We conclude by offering perspectives on studying sociable schedules.

SEASONALLY CHANGING BEHAVIOUR: MECHANISTIC FRAMEWORK

Endogenous Programmes

Most organisms have evolved complex mechanisms to meet the challenge to stay on time, as demonstrated by chronobiology, the systematic study of 'adaptations ... to cope with regular geophysical cycles' (Dunlap et al. 2004, page XVII). Birds have had a pioneering role as subjects in research on timing, and we therefore focus on avian annual cycles (for work on other taxa and timescales, see Conradt & Roper 2003; Davidson & Menaker 2003; DeCoursey 2004; Marques & Waterhouse 2004; Mistlberger & Skene 2004). Observations under constant, favourable conditions imply that birds have endogenous programmes for initiating behaviour at the right time of year (e.g. Naumann 1897–1905; Gwinner 1986, 1996; Berthold 2001). Birds can sustain endogenous programmes over at least 10 years without external cues (Gwinner 1996). These programmes provide the framework for the sequence, progress and expression of life cycle stages (Wingfield & Jacobs 1999). Their truly endogenous, circannual nature is evidenced by period lengths that differ from exactly one calendar year when birds are kept indoors

(Gwinner 1986; Piersma 2002b). However, in nature, birds usually synchronize with the external year in reference to timing cues. Rowan (1926) showed the importance of photoperiod, the annual change in daylength for seasonal behaviour. Daylength has now been identified to provide important 'initial predictive information' for timing of numerous avian species (Hahn et al. 1992, 1997; Hau et al. 1998; Wingfield & Jacobs 1999). Within the 'windows' set by endogenous programmes, schedules are influenced by other proximate factors (Gwinner 1999). Many species adjust timing in response to temperature, weather and food supply (e.g. Lack 1943, 1950, 1968; Perrins 1970; Drent & Daan 1980; Bairlein & Gwinner 1994; Maney et al. 1999; Piersma 2002a; Leitner et al. 2003). Seasonal behaviour is also affected by the availability of commodities, such as nestboxes, which prime reproductive functions (Gwinner et al. 2002; Wingfield & Silverin 2002). Comparatively little is known about the effects of social interactions, however, with the possible exception of sexual cycles (e.g. Lewis & Orcutt 1971; Gwinner 1986, 1999; Wingfield & Marler 1988; Hahn et al. 1997; Goldmann et al. 2004).

The way in which birds respond to temporal information is influenced by their circannual programmes, which function as 'periodically changing dispositions to respond to environmental cues' (Gwinner 1999, page 2367). The current phase of a bird's circannual clock determines how temporal information, for example daylength, is interpreted. Thus, short days generally accelerate seasonal activities in the autumn but delay schedules in spring (e.g. Farner & Gwinner 1980; Hahn et al. 1992, 1997). In Fig. 1 we propose how environmental factors, including social interactions, influence seasonal timing.

Interactions with Social Behaviour

Time programmes influence a bird's social behaviour as well as its receptiveness to conspecifics. In dark-eyed juncos, *Junco hyemalis*, nocturnal restlessness (Zugunruhe), an indicator of the urge to migrate, is obligatory in the autumn but later depends on social and nutritional conditions (Terrill 1987). Reproductive windows, once opened, are fine-tuned in behavioural interactions (Fig. 1). For example, male song sparrows, *Melospiza melodia*, were sexually active in response to steroid-implanted females in spring and summer, but not in autumn (Runfeldt & Wingfield 1985; Wingfield & Monk 1994). The neuroendocrine regulation of social activities, such as seasonal vocal communication, is, in many species, sensitive to photoperiod. Daylength can affect male song, the neuronal responses of conspecifics exposed to it, and even the ability of birds to learn from a vocal tutor (e.g. Ball & Bernard 1997; Whaling et al. 1998; Tramontin et al. 1999; Ball & Bentley 2000; Del Negro et al. 2000). While endogenous time programmes provide the framework for social behaviour, little is known about whether social interactions can in turn phase-shift endogenous programmes (Gwinner 1975, 1986, 1999; Goldmann et al. 2004).

Time programmes are greatly differentiated between species and even populations (see below) to the seasonal



Figure 1. Conceptual model of seasonal timing in birds. The three concentric rings indicate annual changes in the social and physical environments (outermost ring), in the circannual programme (middle ring) and in overt seasonal behaviour such as migration, wintering, breeding and moult (innermost ring). Social and environmental factors affect behaviour (black arrows) via circannual programmes, which provide the framework for a seasonally correct response. Social interactions, such as competition for winter territories, can interact with environmental factors such as poor foraging conditions (bent black arrow). The behavioural response of a bird can create feedback effects (double-headed arrow) by modifying its environmental and social situation (e.g. by continuing migration), which is then newly interpreted via circannual programmes. Eventually, movement of the circannual clock modifies behavioural responses. Inspired by Helms (1963).

context. But schedules within a population are rarely perfectly synchronized. Environmental factors do not act uniformly on all members of a population and individuals differ from each other. Individuals can be characterized by their 'state', that is, the suite of factors determining current behavioural decisions, including the ability to carry out seasonal behaviour. Next to time programmes, known factors include age, sex, condition, genetic background, experience and development, in interaction with environmental conditions such as territory quality, food abundance and social context (Newton 1989; Brown 1996; Houston & McNamara 1999; Carere et al. 2003; West et al. 2003). For example, Sandberg (2003) tested flight directions of migratory passerines before they crossed open ocean. A bird's directional choice, crossing the barrier or turning away from it, was related to its nutritional condition, with knock-on effects on the migration schedule. The exact timing of seasonal activities, in turn, can have feedback effects on state, as shown for effects of laying date on parents and offspring (Nilsson 1999; Thomas et al. 2001). Consequences of temporal behaviour can thereby be carried over across seasons (Houston & McNamara 1999; West et al. 2003; Norris et al. 2004a). Thus, reproductive timing can affect moult timing, which, in turn, can influence subsequent laying date (e.g. Kempenaers 1995; Hemborg & Merilä 1998; Forstmeier et al. 2001). The fact that state both depends on season and affects the ability to perform seasonal behaviour puts it at the interface between endogenous disposition and environment.

BEHAVIOURAL AND EVOLUTIONARY CONTEXT

Forms of Social Information Transfer

Annual cycles of birds require delicate integration of behaviours that all have to take place at the right time and in the right space. Although closely linked, temporal and spatial behaviour have been approached differently by researchers. Whereas timing has been studied with an emphasis on mechanisms, research on spatial behaviour has focused on ecological and social contexts (e.g. Reed et al. 1999; Giraldeau et al. 2002; Doligez et al. 2003; Simons 2004). Insights concerning the contribution of social information to spatial behaviour can also inspire the study of temporal behaviour. Accordingly, some of the information that an animal acquires becomes social information (Danchin et al. 2004; Conradt & Roper 2005; Dall et al. 2005). Some information is provided inadvertently, such as the place and time of breeding and foraging. Birds also exchange information about endogenous dispositions by vocalizations, plumage and ornaments (e.g. Piersma & Jukema 1993; Andersson 1994; Piersma et al. 2001; Gil & Gahr 2002; Delhey et al. 2003). Mere observation of others thus provides temporal cues. Activities, such as staging at a given site, may simply be copied as a shortcut to seasonally correct behaviour without costly trial-and-error learning, but at risk of communal mistakes (Cavalli-Sforza & Feldmann 1981; Wagner & Danchin 2003; Laland 2004). Mistakes can be reduced, such as by information pooling in decision-making

processes (Conradt & Roper 2003, 2005; Simons 2004; Chan 2005; Couzin et al. 2005) or by observing the performance of others ('public information'; Valone 1989; Boulinier & Danchin 1997; but see Giraldeau et al. 2002). Birds actively seek out opportunities to collect public information. Kittiwakes, *Rissa tridactyla*, for instance, prospect for potential breeding sites at the time of richest information on reproductive success (Boulinier et al. 1996) and some songbirds eavesdrop on disputes of their neighbours (Naguib et al. 2004; Peake 2005). By acquiring information from interactions of others, birds thus engage in communication networks.

Active communication (signalling) of seasonal disposition involves complex systems of visual, vocal and possibly olfactory cues (e.g. Lack 1968; Piersma et al. 1990; Gil & Gahr 2002; Hagelin et al. 2003; Bonnadonna & Nevitt 2004). Song and plumage are used not only for signalling in courtship and territorial display, but also in wider social contexts, such as in flocking species to maintain cohesion or attract conspecifics (Brooke 1998; Beauchamp & Heeb 2001; Chan 2005). Communication processes can eventually lead to culture (Danchin et al. 2004; Galef 2004), for example about itineraries in socially migrating birds (Sutherland 1998). Active communication often entails 'involved' interactions, that is, targeted signalling in feedback processes. For instance, birds engage in countersinging and can thereby de-escalate or escalate territorial disputes (Gil & Gahr 2002; Beecher & Brenowitz 2005; Peake 2005). Similarly, mates often display courtship behaviour that stimulates breeding in feedback loops (Brockway 1964, 1965; Lehrmann 1964).

Negotiating Schedules

A bird's behaviour is based on its current disposition, but by being directed at conspecifics, it elicits responses from others, which in turn can affect the bird's own temporal behaviour (Fig. 1). Seasonal activities are thus 'negotiated' in decision-making processes and in social interactions. In territorial disputes, for example, birds negotiate ownership and thereby resources for ensuing life cycle stages. Similarly, socially migrating birds communicate their readiness to move on and thereby negotiate departure time (e.g. Raveling 1969; Rees 1987; Piersma et al. 1990; Chan 2005; Conradt & Roper 2005).

Social interactions can theoretically affect seasonal behaviour in different ways (Lewis & Orcutt 1971), as illustrated for two birds in Fig. 2. The most frequently discussed social effect is synchronization (Fig. 2a) within pairs and especially within large colonies, resulting from information transfer and involved interaction. Interactions can also be stimulating (Fig. 2b) or delaying without erasing timing differences between individuals. In competitive and agonistic interactions (Fig. 2c) successful birds typically advance their schedules at the cost of those that lose resources. In all cases, social interactions can contribute to seasonal timing when individuals differ from each other in schedules and abilities, including information and competitive advantage.

Cooperation and conflict generally have different effects on schedules. Cooperative behaviour tends to

synchronize avian schedules (Fig. 2a, b). In the widest sense, flock and colony formation can represent cooperative behaviours (Conradt & Roper 2003, 2005; Simons 2004). Some cooperative activities can involve kinship, such as migratory flight formation (Andersson & Walander 2004), lekking and communal breeding (Nakagawa & Waas 2004). Caring for mates and offspring often has a large effect on schedules. Social stimulation of breeding has received much attention in the heydays of ethology (e.g. Lorenz 1935; Tinbergen 1953), in the context of coloniality (Fraser Darling 1938; Lewis & Orcutt 1971) and more recently in behavioural endocrinology (Wingfield 1980; Wingfield & Marler 1988). However, it can be difficult to exclude alternative interpretations of what appears to be 'social synchronization'. Individuals could be synchronous because of a common response to environmental factors (Lewis & Orcutt 1971; Ims 1990), just as spatial aggregations may be driven by commodity selection (i.e. the choice of particular resources) rather than by social benefits (Danchin & Wagner 1997; Wagner et al. 2000; Schjørring 2001; Doligez et al. 2003). Alternatively birds could be synchronous because of a common genetic background and assortative mating with partners on similar schedules (e.g. Rees 1987; Davis 1988; Bearhop et al. 2005). Song, display and sophisticated partnership rituals (Croxall 1991; Black 1996a; Hall 2004) could serve either purpose, that is, help to synchronize breeding cycles or to select synchronous mates. Researchers have used different approaches to determine social synchronization. For example, researchers in classical ethology searched for species-specific signalling (e.g. Lorenz 1935; Krebs & Davies 1987; Wachtmeister 2001). Circumstantial evidence for social synchronization is provided by comparisons of synchrony on different spatial scales, for example within and between groups (e.g. Brown & Brown 1996; but see Lewis & Orcutt 1971; Ims 1990). More direct evidence for social stimulation comes from experimental approaches by which cues or schedules were manipulated (see below).

In contrast, conflict, including competition, territoriality and dominance hierarchies, tends to reduce synchrony within a population (Fig. 2c). Although mostly studied in the context of reproduction, conflict can be influential throughout the year, for example to secure food and territories for winter (Wingfield & Silverin 2002; Pravosudov et al. 2003; Studds & Marra 2005). If resources such as feeding and breeding opportunities are limited, primary access is often determined in aggressive encounters. The winners of encounters can carry out the most rewarding seasonal behaviour and sometimes advance their schedules (e.g. Rappole & Warner 1976; Rappole 1995; Moore et al. 2003; Öst et al. 2003; Studds & Marra 2005), whereas the losers may suffer costs of defeat, including delays. Such negotiations can be mediated by hormones: according to the 'challenge hypothesis', territorial conflict temporarily boosts testosterone in winners to secure resources (Wingfield et al. 1990; Gwinner et al. 2002). However, the classification of interactions into cooperation or conflict is a generalization, because they sometimes co-occur, for example within families or between neighbours (e.g. Drent & Daan 1980; Slagsvold 1999; Hyman 2005).

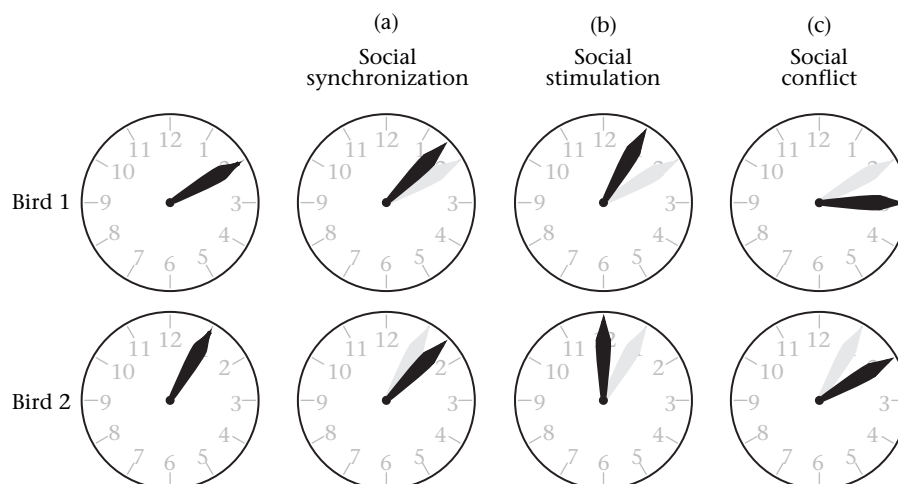


Figure 2. Schematic examples of social effects on overt seasonal behaviour. Two individuals (birds 1 and 2, indicated on upper and lower rows, respectively) initially differ in seasonal schedule, indicated by black hands on the left-hand clocks. Numbers on the clock stand for the progress of seasonal activities (e.g. 1200 indicates the onset of reproductive behaviour, such as arrival at the nest site). The schedule of bird 1 is advanced relative to bird 2, for example if bird 1 starts nest construction while bird 2 still explores for nest sites. After coming into contact, they adjust their schedules (a, b, c: black hands show new schedule, grey hands show initial schedule). (a) The birds synchronize their seasonal activities via a delay of bird 1 and an advance of bird 2. (b) The birds stimulate each other, for example by vocalizing, so that both advance their schedules. (c) Effects of social conflict: after interacting, for example by territorial dispute, bird 2 greatly advances its seasonal behaviour at the cost of bird 1, whose schedule is set back, for example by territory loss to bird 2. Synchrony between the birds increases in (a), remains constant in (b) and decreases in (c).

Costs and Benefits of Sociable Schedules

Time programmes are adaptations that help organisms to cope with fluctuating conditions. To be functional, time programmes must evolve to adjust behaviour to local conditions. Heritabilities suggest substantial potential for the evolution of seasonal timing (Helm & Gwinner 1999, 2001; Merilä & Sheldon 2001; Pulido & Berthold 2003; Sheldon et al. 2003; but see van der Jeugd & McCleery 2002). Evolutionary change could be accelerated by assortative mating of birds with similar time programmes (Rees 1989; Gunnarsson et al. 2004; Bearhop et al. 2005).

Time programmes are responsive to environmental conditions, so they are best understood in the framework of reaction norm and threshold approaches (e.g. Ketterson & Nolan 1983; van Noordwijk 1989; Rees 1989; Adriaensen & Dhondt 1990; Dingle 1996; Pigliucci 2001; Gwinner & Helm 2003; Chan 2005). Fine tuning of population reaction norms has been found in several avian species. Laying dates of blue tits and moult timing of several stonechat taxa (*Saxicola* spp.), for instance, were adjusted to local environments by modified responses to daylength (Silverin et al. 1993; Lambrechts et al. 1996; Helm et al. 2005). Ultimate factors in the evolution of schedules are primarily food availability, climate and predation, but social interactions also contribute (e.g. Lack 1943, 1950, 1968; Immelmann 1971). Territoriality, for example, is thought to drive selection for early arrival at breeding and wintering grounds, and possibly also selection for early moult (e.g. Kalela 1954; Myers 1981; Ketterson & Nolan 1983; Thompson 1991; Rappole 1995; Wingfield & Silverin 2002). The timing of conspicuous signalling (e.g. seasonal song and breeding plumage) is presumably affected by competition and sexual selection. High

breeding synchrony in European starlings, *Sturnus vulgaris*, correlated with a sharp decline in recruitment of late-hatched young. Smith (2004) interpreted these patterns as caused by benefits of immediate flock formation of synchronously fledged young.

Sociable schedules are also thought to be adjusted to life history context. They should occur only when their advantages outweigh disadvantages, apart from facilitation that imposes no apparent costs (Fraser Darling 1938, 1952; Lewis & Orcutt 1971; Ims 1990; Brown & Brown 1996; Bruno et al. 2003). Social information use is thought to convey selective benefits of improved performance (Danchin et al. 2004; Simons 2004; Conradt & Roper 2005; Couzin et al. 2005) and may save time spent on trial and error (Boulinier & Danchin 1997). Possible costs include developing cognitive abilities, allocating time to collect information and risking error and conflicting interests (Alatalo et al. 1988; Reed et al. 1999; Gil & Gahr 2002; Gir-aldeau et al. 2002; Ricklefs 2004). In colonial breeders, selective advantages of reproductive synchronization are thought to include mutual stimulation (Waas et al. 2000, 2005), localization of nestling food (Brown & Brown 1996) and reduced nest predation (Fraser Darling 1938; Immelmann 1971). These benefits depend on context. Nest predation can select for both synchrony and asynchrony of reproduction, depending on predator habits and spatial structure (Ims 1990). Advantages of mutual stimulation may be outweighed by negative density-dependent effects, such as competition for nesting space (e.g. van der Jeugd 2001; Pärt & Doligez 2003). After moult, synchronized departure of eared grebes, *Podiceps nigricollis* (Jehl et al. 2003) causes hundreds of casualties that result from mid-air collisions. Furthermore, sociable schedules may impose synchronization costs (Conradt &

Roper 2003, 2005). Optimal schedules of individuals differ, and synchronization would then imply compromising between individual best temporal solutions.

Conflict accrues costs to losers and winners. Defending and advertising a territory exposes a bird to heightened predation risk, reduces foraging time and is energetically expensive (Gil & Gahr 2002; Ward et al. 2003; Dunn et al. 2004; Goymann & Wingfield 2004a). Conflict should therefore be favoured only when its advantages outweigh disadvantages in reference to the behaviour of others (e.g. Ketterson & Nolan 1983; Wingfield et al. 2001; Hyman 2005). Seasonal change in social behaviour and in sensitivity to social cues is expected to evolve when costs and benefits fluctuate over time (DeCoursey 2004). Many factors known to modify the balance of costs and benefits indeed change with season, for example availability of food and commodities, habitat characteristics, predation risk and time constraints (Immelmann 1971; Alatalo et al. 1988; Reed et al. 1999; Giraldeau et al. 2002; Wu & Giraldeau 2005). Logically, the multitude of potentially selective factors is paralleled by a large variation in sociable schedules in birds.

INTERPLAY BETWEEN SEASONAL AND SOCIAL BEHAVIOUR

Development

Social effects on schedules start with prenatal development (e.g. González-Solís 2004). Social learning can be an important determinant of behavioural transitions (West et al. 2003; Galef 2004; Galef & Heyes 2004; Beecher & Brenowitz 2005). For example, vocal development and territorial behaviour in cowbirds, *Molothrus ater*, required initialization by social stimuli ('social gateways'; West et al. 2003). Depending on social context, the cowbirds developed along different trajectories with knock-on effects on schedules. Their behaviour towards the next generation was similar to their own upbringing, so developmental schedules and behavioural phenotypes were culturally transmitted (Freeberg 1998; West et al. 2003). Similarly, in some species the rate of development of song and sexually mature behaviour is influenced by feedback from same-sex tutors and opposite-sex audience and by trial liaisons (e.g. Whaling et al. 1998; Smith et al. 2000; van der Jeugd & Blaakmeer 2001; Beecher & Brenowitz 2005). Social interactions can also slow development. Aggression presumably selects for delayed maturation, for example of adult plumage (Thompson 1991; Berggren et al. 2004). Competition between siblings counteracts synchrony: by monopolizing resources and by overt aggression, winners may accelerate their own growth while slowing or terminating the development of siblings (Starck & Ricklefs 1998).

Breeding

Birds acquire cues for breeding by watching and overhearing others (e.g. Brown & Brown 1996; West et al. 2003; Danchin et al. 2004; Galef 2004; Zentall 2004).

Parasitic species are remarkably good at synchronizing egg laying with their hosts (Forslund & Larsson 1995; Andersson & Åhlund 2000; Davies 2000; Lyon 2003). Heterospecific attraction to residents can guide settlement decisions of some arriving migrants which gain fitness and advance laying date when they associate with residents (Forsman et al. 2002).

Conspecific information transfer is frequently achieved by active signalling. Plumage of dichromatic species advertises a readiness to breed (e.g. Jenni & Winkler 1994; Wingfield & Silverin 2002) and is also involved in signalling, for instance in courtship displays (e.g. Petrie & Williams 1993). Seasonal vocalizations address competitors, as well as potential mates, and convey differentiated information (Gil & Gahr 2002; Baker 2004; Nelson & Soha 2004; Beecher & Brenowitz 2005; Peake 2005). Concerted competitive displays, for instance in lekking species (Höglund & Alatalo 1995), synchronize breeding although these displays typically enable only a small proportion of the males involved to reproduce. In such displays, synchrony between males is crucial. Among cooperative breeders, synchronization of reproductive behaviour is differentiated. Whereas sexual behaviour is exercised only by dominant individuals, parental care is also provided by helpers. Some evidence suggests that helpers are fully synchronous with the dominant pair but are kept from sexual behaviour by social mechanisms (Wingfield & Marler 1988; Ims 1990; Cockburn 1998; Wingfield & Silverin 2002; Baker 2004). Conspecific information transfer between colonial birds can create a 'culture' of timing. Well-known examples are communal flight displays which presumably synchronize breeding (Fraser Darling 1938; Chapin 1954; Chapin & Wing 1959; Veen 1977; Ims 1990; Brown & Brown 1996). Some highly social species breed successfully only in the presence of conspecifics (e.g. Brockway 1964, 1965; Wingfield & Marler 1988). Mutual stimulation has been suggested to accelerate preparations for breeding and facilitate it at unusual times, even in the autumn (Hahn et al. 1997). Experimental application of social cues generally led to conspecific stimulation (e.g. Ims 1990; Waas et al. 2000, 2005). Waas et al. (2000) found additional, counteracting density-dependent effects in royal penguins, *Eudyptes schegeli*: aggression increased in penguins exposed to playback of conspecific calls.

Social benefits of information transfer and population synchrony possibly occur even in territorial species. Although competitive interactions generally desynchronize schedules, they can also stimulate conspecifics through information and 'challenge' effects (Fraser Darling 1952; Wingfield et al. 1990; Smith 2004; Peake 2005). Males of many species trade off benefits of gaining extrapair paternity in neighbouring territories against the risk of losing paternity to other males during their absence (Petrie & Kempenaers 1998). The degree of breeding synchrony, that is, the proportion of females that is reproductively active at the same time (Björklund & Westman 1986; Kempenaers 1993), might be a driving force behind variation in the level of extrapair paternity. However, intraspecific studies have produced mixed evidence for this idea (Ims 1990; Griffith et al. 2002). An intriguing possibility is

Table 1. Evidence for social effects on avian schedules

Seasonal context	Social context	Type of behaviour	Affected trait	Presumed effect on timing	Source
Development	Conspecific, siblings	Competitive interactions	Growth, maturation	Negotiation of schedules for growth and maturation	Thompson 1991; Starck & Ricklefs 1998; Berggren et al. 2004
Development, breeding	Conspecific	Adult vocal and territorial behaviour	Song, territoriality, age at first breeding	'Social gateway'; initiation or stimulation of development	Whaling et al. 1998; Smith et al. 2000; West et al. 2003; Beecher & Brenowitz 2005
Development, breeding	Pair	Prior pair bond	Age at reproduction, timing of breeding	Pair bond encourages breeding early in life or in the breeding season	Lewis & Orcutt 1971; Black & Owen 1995; Black et al. 1996; Black 1996a, b; van der Jeugd & Blaakmeer 2001; McGraw & Hill 2004
Breeding	Heterospecific	Eavesdropping	Timing of breeding preparations	Synchronization of parasitic species to host	Forslund & Larsson 1995; Andersson & Åhlund 2000; Davies 2000; Lyon 2003
Breeding	Flock, colony, conspecific	Communal flight displays, prospecting/eavesdropping	Timing of breeding	Synchronization; advancement	Fraser Darling 1938, 1952; Chapin 1954; Brockway 1964, 1965; Ims 1990; Brown & Brown 1996; Reed et al. 1999; Waas et al. 2000, 2005
Breeding	Conspecific	Lekking	Timing of breeding	Synchronization	Höglund & Alatalo 1995
Breeding	Conspecific	Male song and display	Male breeding schedules	Negotiation and possibly advancement	Wingfield et al. 1990; Gwinner et al. 2002; Mota & Depraz 2004
Breeding	Conspecific, pair	Male song and display	Female breeding schedules	Advancement and progress	Lewis & Orcutt 1971; Wingfield & Marler 1988; Ims 1990; Bentley et al. 2000; Waas et al. 2000, 2005; Gwinner et al. 2002
Breeding	Pair	Presence of female	Male sexual traits	Progress	Gwinner 1975; Tramontin et al. 1999; Wingfield & Silverin 2002
Breeding	Pair	Feedback between partners	Timing of breeding	Advancement and progress	Brockway 1964, 1965; Lehrmann 1964; Lewis & Orcutt 1971; Croxall 1991; Black 1996a, b; Riebel 2003; Gorissen & Eens 2004; Hall 2004
Breeding	Pair	Partnership behaviour	Timing of breeding	Synchronization to mate with different schedule	Miller 1962; Lehrmann 1964; Davies et al. 1969; Hahn et al. 1997
Breeding	Offspring	Visual exposure to nest, eggs and young	Timing of breeding	Progress of breeding stages, delayed termination	Lewis & Orcutt 1971; Wingfield & Farner 1979; Hahn et al. 1992; Lea et al. 1997
Breeding, moult	Pair	Sex-steroid implanted partner	Termination of breeding, moult onset	Delayed end of breeding state, delayed moult onset	Runfeldt & Wingfield 1985; Düttmann et al. 1999; Ketterson et al. 2001
Breeding, moult	Parent—offspring	Late breeding, increased parental effort	Parental moult and next-year breeding	Delayed moult; sometimes carry-over to next-year breeding	Newton 1966; Morton & Morton 1990; Siikamäki et al. 1994; Hemborg & Lundberg 1998; Hemborg & Merilä 1998; Norris et al. 2004b
Moult	Pair	Unknown mechanism	Coordinated moult	Synchronized with mate	Owen & Ogilvie 1979; Larsson 1996
Moult, migration	Parent—offspring	Timing of offspring fledging	Onset of parental moult, migration	Synchronized with young	Larsson 1996; Loonen 1997
Moult, migration	Conspecific	Social aggregation	Timing of moult and subsequent departure	Synchronized in flock	Piersma 1988; Jehl 1990; Jehl et al. 2003

(continued on next page)

Table 1 (continued)

Seasonal context	Social context	Type of behaviour	Affected trait	Presumed effect on timing	Source
Moult, wintering	Conspecific	Autumn territorial establishment	Timing of moult and territorial behaviour?	Negotiation of moult schedules?	Suggested by Dhondt 1973
Migration	Flock	Communal flight displays, calling	Timing of activities and departure	Synchronization and recruitment of flock	Raveling 1969; Black 1988; Piersma et al. 1990; Brooke 1998; Beauchamp & Heeb 2001; Conradt & Roper 2003, 2005; Chan 2005
Migration	Flock, family	Communal migration	Migration timing and route	Cultural transmission of itinerary	Sutherland 1998; Chernetsov et al. 2004
Migration	Flock	Group navigation	Migration timing and route	Presumably faster and more efficient	Hamilton 1967; Wallraff 1978; Tamm 1980; Chernetsov et al. 2004; Simons 2004; Conradt & Roper 2005; Couzin et al. 2005
Migration	Pair	Partnership behaviour	Migration timing and route	Synchronization and coordination	Rockwell & Cooke 1977; Rees 1987, 1989; Rohwer & Anderson 1988; Black 1996a b; Chan 2005
Migration, wintering, breeding	Heterospecific, conspecific	Dominance-mediated access to high-quality food and territories	Migratory schedules, timing of Zugunruhe	Negotiation of migration progress, departure from winter grounds and arrival on breeding grounds	Rappole & Warner 1976; Gauthreaux 1978; Ketterson & Nolan 1983; Terrill 1987; Rappole 1995; Moore et al. 2003; Sandberg 2003; Norris et al. 2004a; Studds & Marra 2005
Migration, breeding	Pair	Unknown mechanism	Arrival on separate routes	Synchronization	Davis 1988; Gunnarsson et al. 2004
Migration, breeding	Heterospecific, conspecific	Attraction to settlement location	End of migration, reproductive timing	Advanced or informed settling, earlier breeding	Helms 1963; Brown & Brown 1996; Forsman et al. 2002; Hahn & Silverman, in press

that relative costs and benefits of extrapair paternity for both males and females modify the degree of breeding synchrony in a frequency-dependent manner.

Breeding partners typically coordinate their schedules. Female schedules were advanced by playback of male song in the laboratory and the field (e.g. Bentley et al. 2000; Mota & Depraz 2004). In experimental studies, the importance of social cues for reproduction differed between the sexes. Whereas males reached full reproductive state when kept individually, females often required mates for complete gonadal activation (Wingfield & Marler 1988; Wingfield et al. 2000). Male reproductive development was none the less enhanced and accelerated by females (e.g. Gwinner 1975; Tramontin et al. 1999; Wingfield & Silverin 2002). Males tended to have longer time windows for reproduction and accommodated to females, which gave the start signals for pair coordination. Crossbreeding of goose species with different schedules had marked effects on the onset of breeding in males but not females (Davies et al. 1969). Male but not female song sparrows modified breeding schedules when their mates were manipulated by sex steroid implants: males elevated

sex-steroid levels and delayed moult by a month in response to prolonged sexual solicitation by oestradiol-treated females (Runfeldt & Wingfield 1985; Ketterson et al. 2001). However, pair synchronization differs between species, possibly in relation to the social system (Runfeldt & Wingfield 1985; Hahn et al. 1997). In shelducks, *Tadorna tadorna* (Düttmann et al. 1999), testosterone implants in males delayed their moult as well as that of their female partners. In contrast, gonadal and moult cycles of captive African stonechats were unaffected by the presence of a mate (Gwinner et al. 1995). Finally, in European starlings availability of nestboxes appeared to influence male reproductive schedules more than did the presence of a mate (Gwinner 1975; Gwinner et al. 2002).

Feedback processes between mates have been thoroughly documented (e.g. Lorenz 1935; Tinbergen 1953; Lewis & Orcutt 1971; Wingfield & Marler 1988; Black 1996a; Wachtmeister 2001). In addition to visual displays, this coordination can involve interactive vocalization, not just in duetting species, but also during the dawn chorus (Ball & Balthazart 2001; Gil & Gahr 2002; Riebel 2003; Gorissen & Eens 2004; Hall 2004). Feedback between

mates often results in close synchronization between ovulation and male advertising and mate guarding (Moore 1982; Wingfield et al. 2000). Females should determine the precise time of breeding, accounting for state and year-to-year differences in environmental conditions, because their reproductive schedules are often limited by resource availability (Wingfield 1980; Moore 1982; Stevenson & Bryant 2000; Chastel et al. 2003; Drent et al. 2003). Once clutches are laid, exposure to eggs and begging chicks can trigger parental behaviour and thereby affect and synchronize parental schedules (Wingfield & Farner 1979; Davis 1988; Lea et al. 1997). These studies refer to 'typical' avian sex roles with male-biased territorial and competitive behaviour. It is not clear whether results can be generalized to species in which females take the lead in competition for mates and territories (e.g. Wingfield & Silverin 2002; Goymann & Wingfield 2004b).

Field data point to considerable benefits of temporal coordination between breeding partners. Earlier laying among birds with long-term pair bonds is common in waterfowl and seabirds (Black & Owen 1995; Black 1996a, b; Black et al. 1996) and has also been reported in passerines (McGraw & Hill 2004). Advantages of temporal coordination are suspected to be a driving factor for maintaining monogamy, especially in unpredictable environments (Miller 1962; Immelmann 1971; Black 1996b; Hahn et al. 1997). Davis's (1988) research on Adélie penguins, *Pygoscelis adeliae*, revealed the highest breeding success among well-synchronized pairs, while divorce rate was highest among birds with uncoordinated routines. Davis suggested that the penguins mated assortatively to synchronize their schedules (cf. Bearhop et al. 2005).

Moult

Although not commonly considered a social activity, moult also occurs in social contexts. Many species assemble for moult, sometimes after long migrations to special sites. Moult aggregations can be formidable (Piersma 1987; Jehl 1990; Jehl et al. 2003), but little is known of their behavioural ecology and whether they accrue social benefits. Birds may gather to capitalize on abundant food and to reduce predation risk (Piersma et al. 1988; Jehl 1990; Düttmann et al. 1999), especially during flightless periods. Great crested grebes, *Podiceps cristatus*, flock for wing moult but are otherwise territorial. An odd simultaneous change of ornamental head feathers, used in display, suggests that, in this species, social interactions do play a role during moult aggregations (Piersma 1988).

Reproductive events exert strong influences on moult timing. Passerines, which in seasonal habitats tend to avoid overlapping activities, often delay moult when breeding late in the year. Delays can increase with parental effort. The costs of such compromised schedules appear to counteract synchronization among breeding partners and can become subject to sexual conflict (e.g. Newton 1966; Siikamäki et al. 1994; Nilsson & Svensson 1996; Hemborg & Lundberg 1998; Hemborg & Merilä 1998; Slagsvold 1999; Dawson et al. 2000; Norris et al. 2004b). Whereas late-breeding females often delay moult while

provisioning chicks, males tend to initiate moult on time and sometimes desert nestlings (Ezaki 1988). However, fathers contributing to nestling care tend also to postpone or extend moult (Morton & Morton 1990; Norris et al. 2004b). Delayed moult of late-breeding and re-nesting birds has been attributed to inhibitory effects of sex steroids. Sex steroids could be boosted by cues from clutches but also from mates, as suggested by studies done in the context of breeding (Runfeldt & Wingfield 1985; Düttmann et al. 1999). Delays also result from resource constraints (Morton & Morton 1990; Hahn et al. 1997; Borrás et al. 2004). Synchronization within families can be pronounced in species with extended brood care. In the barnacle goose, *Branta leucopsis*, timing of wing moult is synchronized between breeding partners so that both pair members regain flight at the same time (Larsson 1996; Düttmann et al. 1999). This correlation is weaker in pairs that reared young, perhaps because carry-over effects of breeding differ between the sexes. In Arctic populations of barnacle geese, wing moult is timed so that parents regain flight precisely when their offspring fledge. However, this synchronization has broken down in a recently established southerly population, because breeding has advanced more than wing moult (Larsson 1996; Loonen 1997).

Social interactions are thought to select for the timing of prenuptial moult, during which dichromatic species change into breeding plumage (Figuerola & Jovani 2001; Wingfield & Silverin 2002). Breeding plumages signal to competitors and prospective mates alike and should therefore evolve as a compromise between social benefits and costs (e.g. Thompson 1991; Berggren et al. 2004). Proximally, bright nuptial plumages may depend on a bird's state and could therefore contribute to honest signalling (e.g. Peters et al. 2000; Piersma et al. 2001; Wingfield & Silverin 2002; Hill 2002). Dhondt (1973) suggested a trade-off between moult and territorial defence in the autumn. Great tits may have to choose between establishing a winter territory first or moulting first. A late moult may accrue costs, including shorter wings, but failure to attain a territory may threaten winter survival. The tits' moult schedules may therefore be negotiated in competitive interactions over territory ownership.

Migration

Social interactions strongly affect migratory schedules. Many species are sociable during migration even if they are otherwise highly territorial. Some tolerate conspecifics during flight phases but not at staging grounds (e.g. Rappole & Warner 1976; Rappole 1995; Chan 2005). However, even solitary migrants use social cues, for instance conspecific and heterospecific attraction to stopover sites and destinations (Rappole 1995; Danchin & Wagner 1997; Forsman et al. 2002; Hahn & Silverman, in press). Sociable migrants have inspired theoretical approaches to communal decision making and information pooling (Wallraff 1978; Conradt & Roper 2003, 2005; Simons 2004; Couzin et al. 2005). Flocking for migration may enhance orientation and performance (Hamilton 1967;

Tamm 1980; Chernetsov et al. 2004; Chan 2005) and reduce flight costs (Lissaman & Shollenberger 1970; Badgerow & Hainsworth 1981; Cutts & Speakman 1994; Andersson & Wallander 2004). Flocking species sometimes display preflight signalling before initiating migration (e.g. Raveling 1969; Black 1988). Synchronized round flights and intense vocal activity precede and accompany the departure of shorebirds for long-distance flights, which they undertake in highly structured formations (Piersma 1983; Piersma et al. 1990). That these displays may act to recruit and synchronize population members is suggested by the observation that shorebirds departed from a coastal site in bigger flocks when more birds of similar size and shape (mostly conspecifics) were available (Piersma et al. 1990). This observation is consistent with the hypotheses that advantages of flying in large flocks encourage synchronization and that with increasing dissimilarity, synchronization costs may offset benefits (Conradt & Roper 2003, 2005).

Family influences on migration schedules are pervasive. In species with extended brood care, especially waterfowl, parents actively determine the time course of migration of their offspring. Migratory itineraries are thus culturally transmitted, backed by endogenous programmes (e.g. Rees 1989; Sutherland 1998; Chernetsov et al. 2004). In species with long-term pair bonds, closely coordinated arrival of the partners favours early laying (Lewis & Orcutt 1971). Coordinated arrival can be achieved by travelling together. For example, in several goose species, males and females pair on the winter grounds. The male then accompanies his mate to her natal colony and accommodates to local conditions (Rockwell & Cooke 1977; Rohwer & Anderson 1988). Males, in turn, influence autumn migration (Rees 1987). Coordinated arrival also occurs in species where the sexes differ in migration and wintering (Davis 1988; Black 1996a, b). Male black-tailed godwits, *Limosa limosa* returned slightly before females, but arrival dates of mates were closely correlated (Gunnarsson et al. 2004). Identified pairs had wintered on average almost 1000 km apart and were never observed together on migration. The mechanisms by which these pairs coordinate arrival are unknown, but endogenous programmes are almost certainly involved. Coordinated arrival could be based on prior synchronization preserved by accurate time keeping. Mates could also have inherently similar time programmes, possibly through assortative mating (Davis 1988), as recently shown in the blackcap, *Sylvia atricapilla* (Bearhop et al. 2005).

Competition and dominance are thought to influence migratory behaviour and distance. Differences in distance, in turn, affect seasonal schedules: longer journeys are typically associated with later arrival on the breeding grounds. In partially migrating species, only some individuals leave the breeding grounds. Individual differences may result from competition, such as for winter territories, by which dominant birds force subordinates to (e)migrate (Lack 1943–1944; Kalela 1954; Gauthreaux 1978; Ketterson & Nolan 1983; Adriaensen & Dhondt 1990; Schwabl & Silverin 1990). Similarly, in differential migrants, population members travel over various distances, and subordinates may have to fly further than dominants.

These ideas have been proposed because migrant proportions and migration distances are often higher among presumably subordinate birds, that is, in younger birds, in the subordinate sex and in late-hatched young (Lack 1943–1944; Gauthreaux 1978; Adriaensen & Dhondt 1990; Schwabl & Silverin 1990). However, differences between population members can often be alternatively explained by migration programmes, developmental processes and differences in state (Ketterson & Nolan 1983; Schwabl & Silverin 1990; Holberton 1993; Berthold 2001; Drent et al. 2003).

Direct evidence for dominance effects on migration schedules comes from observations of individuals and experimental approaches. Removal experiments showed that American redstarts, *Setophaga ruticilla*, overwintering in superior territories built up greater fat reserves and departed for return migration earlier in the spring (Studds & Marra 2005). Staging territories of northern waterthrushes, *Seiurus noveboracensis*, were also vigorously defended (Rappole & Warner 1976): birds that obtained feeding territories continued their stopover whereas those that did not moved on. Similarly, captive migrants increase Zugunruhe when food is scarce (Biebach 1985). In dark-eyed juncos, this behaviour, interpreted as a readiness to resume migration, can be triggered by dominant conspecifics (Terrill 1987). However, dominance may depend on state. Moore et al. (2003) found that in captive migrant red-eyed vireos, *Vireo olivaceus*, dominant birds controlled access to food. However, when subordinates were starved, they were able to secure the greater share of food. These examples show that competition and conflict can affect the progress and timing of migration.

PROSPECTS FOR THE STUDY OF SOCIABLE SCHEDULES

Sociable schedules are ubiquitous but largely unstudied. Technological and conceptual advances promise exciting progress in future research. Ecological studies can benefit from rapidly developing animal-tracking methods. As transmitters become increasingly smaller and more affordable, and as geographical information technology gets more refined, we may soon be able to track social behaviour over time. For example, flock size and cohesion can change considerably during migration and wintering, presumably related to costs and benefits such as intraspecific competition and predator detection (e.g. Myers 1983, 1984; Piersma et al. 1990, 1993; Whitfield 2003). Radio-tracking of individuals over time can relate birds' social activities to changes in potentially relevant environmental factors (e.g. Warnock & Takekawa 2003). A long-term perspective of such studies could include interspecific comparisons to identify key factors in the evolution of sociable schedules. Our knowledge is still mostly deficient about many potentially involved factors (Ims 1990). Particular questions, such as temporal aspects of song learning and sustained partnerships (Black 1996a, b; Ens et al. 1996; Beecher & Brenowitz 2005), are already suitable for comparative analyses, and models for communal

decision making apply to migratory birds (Conradt & Roper 2003, 2005; Simons 2004; Chan 2005; Couzin et al. 2005).

In ecophysiology, field endocrinology could further elucidate interactions between social and seasonal behaviour. Hormones set the stage for seasonal behaviour and mediate effects of conspecifics and environmental factors on schedules (e.g. Wingfield & Marler 1988; Landys-Cianelli et al. 2002; Wingfield & Silverin 2002). Understanding cues for seasonal timing is incomplete without considering the physiological mechanisms that determine and possibly constrain avian responses (Gil & Gahr 2002; Ricklefs & Wikelski 2002; Piersma 2002a). This realization is fuelling an interest in combining ecological and endocrinological approaches. New methods in field endocrinology, if validated, could offer new research avenues (e.g. Hiebert et al. 2000; Altmann & Altmann 2003; reviewed in Bauchinger et al. 2005).

The field of ecological genetics (e.g. Conner & Hartl 2004) is also providing new opportunities. Sampling methods now offer techniques to assess kin relationships (Piertney et al. 2000), and quantitative genetic tools have become suitable for the study of inheritance in wild populations (Merilä & Sheldon 2001; Pulido & Bertoldo 2003; Sheldon et al. 2003; Kruuk 2004; Nakagawa & Waas 2004). These developments help to approach the evolution of sociable schedules from two sides. Molecular sampling can detect kinship patterns of temporal behaviour and quantitative methods can estimate its genetic control and evolvability. Together, these techniques allow researchers to approach the evolution of timing in social contexts. Contributions of endogenous programmes can be contrasted with learning and, in some species, culture. For example, the relative importance of prolonged parental care for the cultural transmission of schedules is poorly understood. The relative contributions of genes and culture can be disentangled by cross-fostering and its natural counterparts, intraspecific brood parasitism and adoption. These processes occur widely in species with prolonged parental care, notably waterfowl (e.g. Forslund & Larsson 1995; Andersson & Åhlund 2000). Distinguishing between genetic offspring and foster chicks will improve estimates of both the heritability of timing and the importance of cultural transmission. Furthermore, the influences of heritable endogenous rhythms and social stimulation meet where related birds maintain close spatial proximity. Although benefits of spatial aggregations have been extensively studied, possible synchronization by breeding close to relatives, to our knowledge, has not been investigated. If closely related individuals have similar endogenous programmes, kin clustering would be accompanied by synchronization and could thereby accelerate evolutionary adjustments of timing.

Studies of sociable schedules can contribute to urgent questions in behavioural and ecological research. Quickly changing global environments raise concerns about whether organisms can accommodate their behaviour. Changes in phenology, for example earlier springs, may be detrimental to correct timing (Visser et al. 1998; Visser & Lambrechts 1999; Hughes 2000; Walther et al. 2002). Social information could enhance the speed and extent

of such adjustments. Social learning has received much attention and has been shown to be important, especially in birds (reviewed in Galef & Heyes 2004; Beecher & Brenowitz 2005). Effects of time-sense learning (Zeitgedächtnis, DeCoursey 2004), combined with information transfer, on the ability to adjust to environmental change are largely unexplored. Conceivable ways by which birds can culturally transmit changing schedules rest on their active communication of calendars. For example, blue tits partly compensated for mistimed breeding in relation to the food peak by learning from experience obtained in the previous year (Grieco et al. 2002). Tits actively vocalize their breeding disposition, so their learning achievements could be rapidly conveyed to conspecifics. Whether conspecifics make use of such information partly depends on the rigidity of their endogenous programmes and on mechanisms driving reproduction. In more sociable species, 'family traditions' are likely to shape behaviour in largely unknown ways (van der Jeugd et al. 2002; Danchin et al. 2004; Komdeur et al. 2004; Nakawaga & Waas 2004). Sociable long-distance migrants such as geese and shorebirds are therefore intriguing study subjects for adjustments to global change. Cultural transmission may have already helped migrants establish itineraries to newly available staging and wintering areas (Sutherland 1998).

Another emerging central theme in behaviour and ecology, the use of information (e.g. Danchin et al. 2004; Couzin et al. 2005; Dall et al. 2005), can benefit from considering sociable schedules. Research has focused on spatial patterns and largely ignored time, despite acknowledging that anticipation of environments is crucial. Space and time are complementary dimensions, however, that together determine the success of behaviour. For instance, benefits of aggregation depend on the ability of animals to coordinate their schedules (Conradt & Roper 2003, 2005). Birds prospecting for territories visited them at times of particularly high information content (Boulinier et al. 1996; Doligez et al. 2003). Prospectors were apparently aware of schedules and may have collected temporal information along with spatial cues. Time-constrained birds, on the other hand, are thought to spend little time on collecting information (e.g. Alatalo et al. 1988; Reed et al. 1999; Veen et al. 2001). The value of social information may thus be strongly affected by the temporal context of its availability and collection (Doligez et al. 2003; Chan 2005). Consideration of timing could enrich the study of information use in several ways. On the one hand, temporal behaviour differs from spatial behaviour by its physiological organization. Theories based on ideal free decisions may therefore be limited in explaining timing mechanisms, such as rigid calendars and carry-over effects on schedules. On the other hand, inclusion of timing cues adds another dimension to social information and could reveal a greater functional context of behavioural interactions. Interactions between space and time could be included in emerging concepts and models of animal decisions (e.g. Couzin et al. 2005; Dall et al. 2005; but see Conradt & Roper 2005).

Studying sociable schedules is timely and can enrich the study of animal behaviour. Chronobiological studies can also profit from an inclusion of social behaviour. Social

modulation offers mechanisms that allow individually hard-wired time programmes to function efficiently in the communal context of free-living animals. Animal behaviour, in turn, could gain a better understanding of rigid and plastic social behaviour, of adjustments to changing temporal conditions, of the relative importance of genetic and cultural inheritance and of scopes and limits of social information use.

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References

- Adriaensen, F. & Dhondt, A. 1990. Population dynamics and partial migration of the European robin (*Erithacus rubecula*) in different habitats. *Journal of Animal Ecology*, **59**, 1077–1090.
- Alatalo, R. V., Carlson, A. & Lundberg, A. 1988. The search cost in mate choice of the pied flycatcher. *Animal Behaviour*, **36**, 289–291.
- Alerstam, T. 1990. *Bird Migration*. Cambridge: Cambridge University Press.
- Altmann, S. & Altmann, J. 2003. The transformation of behaviour in field studies. *Animal Behaviour*, **65**, 413–423.
- Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.
- Andersson, M. & Åhlund, M. 2000. Host–parasite relatedness shown by protein fingerprinting in a brood parasitic bird. *Proceedings of the National Academy of Sciences, U.S.A.*, **97**, 13188–13193.
- Andersson, M. & Wallander, J. 2004. Kin selection and reciprocity in flight formation? *Behavioral Ecology*, **15**, 158–162.
- Badgerow, J. P. & Hainsworth, F. R. 1981. Energy savings through formation flight? A re-examination of the VEE formation. *Journal of Theoretical Biology*, **93**, 41–52.
- Bairlein, F. & Gwinner, E. 1994. Nutritional mechanisms and temporal control of migratory energy accumulation in birds. *Annual Reviews of Nutrition*, **14**, 187–215.
- Baker, A. J., Gonzalez, P. M., Piersma, T., Niles, L. J., de Lima Serano do Nascimento, I., Atkinson, P. W., Clark, N. A., Minton, C. D., Peck, M. K. & Aarts, G. 2003. Rapid population decline in red knots: fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. *Proceedings of the Royal Society of London, Series B*, **271**, 875–882.
- Baker, M. C. 2004. The chorus song of cooperatively breeding laughing kookaburras (Coraciiformes, Halcyonidae: *Dacelo novaeguineae*): characterization and comparison among groups. *Ethology*, **110**, 21–35.
- Ball, G. & Balthazart, D. 2001. Ethological concepts revisited: immediate early gene induction in response to sexual stimuli in birds. *Brain, Behaviour and Evolution*, **57**, 252–270.
- Ball, G. & Bentley, G. 2000. Neuroendocrine mechanisms mediating the photoperiodic and social regulation of seasonal reproduction in birds. In: *Reproduction in Context: Social and Environmental Influences on Reproductive Physiology and Behavior* (Ed. by K. Wallen & J. Schneider), pp. 129–158. Cambridge, Massachusetts: MIT Press.
- Ball, G. & Bernard, D. 1997. Photoperiodic and endocrine regulation of seasonal plasticity in the vocal control system of European starling. In: *Perspectives in Avian Endocrinology* (Ed. by S. Harvey & R. Etches), pp. 133–147. Bristol: Journal of Endocrinology Press.
- Bauchinger, U., Goymann, W. & Jenni-Eiermann, S. (Eds) 2005. *Bird Hormones and Bird Migrations. Analyzing Hormones in Droppings and Egg Yolks and Assessing Adaptations in Long-distance Migration*. New York: New York Academy of Sciences.
- Bearhop, S., Fiedler, W., Furness, R. W., Votier, S. C., Waldron, S., Newton, J., Bowen, G. J., Berthold, P. & Farnsworth, K. 2005. Assortative mating as a mechanism for rapid evolution a migratory divide. *Science*, **310**, 502–504.
- Beauchamp, G. & Heeb, P. 2001. Social foraging and the evolution of white plumage. *Evolutionary Ecology Research*, **3**, 703–720.
- Beecher, M. & Brenowitz, E. 2005. Functional aspects of song learning in songbirds. *Trends in Ecology and Evolution*, **20**, 143–149.
- Bentley, G., Wingfield, J. C., Morton, M. & Ball, G. C. 2000. Stimulatory effects on the reproductive axis in female songbirds by conspecific and heterospecific male song. *Hormones and Behavior*, **37**, 179–189.
- Berggren, A., Armstrong, D. & Lewis, R. 2004. Delayed plumage maturation increases overwinter survival in North Island robins. *Proceedings of the Royal Society of London, Series B*, **271**, 2123–2130.
- Berthold, P. 2001. *Bird Migration: a General Survey*. 2nd edn. Oxford: Oxford University Press.
- Biebach, H. 1985. Sahara stopover in migratory flycatchers: fat and food affect the time program. *Experientia*, **41**, 695–697.
- Björklund, M. & Westman, B. 1986. Mate-guarding in the great tit: tactics of a territorial forest-living species. *Ornis Scandinavica*, **17**, 99–105.
- Black, J. M. 1988. Preflight signaling in swans: a mechanism for group cohesion and flock formation. *Ethology*, **79**, 143–157.
- Black, J. M. (Ed.) 1996a. *Partnerships in Birds: the Study of Monogamy*. Oxford: Oxford University Press.
- Black, J. M. 1996b. Introduction: pairbonds and partnerships. In: *Partnerships in Birds: the Study of Monogamy* (Ed. by J. M. Black), pp. 3–20. Oxford: Oxford University Press.
- Black, J. M. & Owen, M. 1995. Reproductive performance and assortative pairing in relation to age in barnacle geese. *Journal of Animal Ecology*, **64**, 234–244.
- Black, J. M., Choudhury, S. & Owen, M. 1996. Do barnacle geese benefit from lifelong monogamy? In: *Partnerships in Birds: the Study of Monogamy* (Ed. by J. M. Black), pp. 91–117. Oxford: Oxford University Press.
- Bonnadonna, F. & Nevitt, G. 2004. Partner-specific odor recognition in an Antarctic seabird. *Science*, **306**, 835.
- Borras, A., Cabrera, T., Cabrera, J. & Senar, J. C. 2004. Interlocality variation in the speed of moult in the citril finch *Serinus citrinella*. *Ibis*, **146**, 14–17.
- Boulinier, T. & Danchin, E. 1997. The use of conspecific reproductive success for breeding patch selection in terrestrial migratory species. *Evolutionary Ecology*, **11**, 505–517.
- Boulinier, T., Danchin, E., Monnat, J.-Y., Doutrelant, C. & Cadiou, B. 1996. Timing of prospecting and the value of information in a colonial breeding bird. *Journal of Avian Biology*, **27**, 252–256.
- Brockway, B. F. 1964. Social influences on reproductive physiology and ethology of budgerigars (*Melopsittacus undulatus*). *Animal Behaviour*, **12**, 493–501.
- Brockway, B. F. 1965. Stimulation of ovarian development and egg laying by male courtship vocalization in budgerigars (*Melopsittacus undulatus*). *Animal Behaviour*, **13**, 575–578.

- Brooke, M. D. 1998. Ecological factors influencing the occurrence of 'flash marks' in wading birds. *Functional Ecology*, **12**, 339–346.
- Brown, C. & Brown, M. 1996. *Coloniality in the Cliff Swallow. The Effect of Group Size on Social Behavior*. Chicago: University of Chicago Press.
- Brown, C. & Brown, M. 2000. Weather-mediated natural selection on arrival time in cliff swallows (*Petrochelidon pyrrhonota*). *Behavioral Ecology and Sociobiology*, **47**, 339–345.
- Brown, M. 1996. Assessing body condition in birds. In: *Current Ornithology*. Vol. 13 (Ed. by V. Nolan, Jr & E. Ketterson), pp. 67–101. New York: Plenum.
- Bruno, J., Stachowicz, J. & Bertness, M. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution*, **18**, 119–125.
- Carere, C., Groothuis, T., Möstl, E., Daan, S. & Koolhaas, J. 2003. Fecal corticosteroids in a territorial bird selected for different personalities: daily rhythm and the response to social stress. *Hormones and Behavior*, **43**, 540–548.
- Cavalli-Sforza, L. L. & Feldmann, M. W. 1981. *Cultural Transmission and Evolution: A Quantitative Approach*. Princeton, New Jersey: Princeton University Press.
- Chan, K. 2005. Partial migration in the silvereye (*Zosteropidae*: Aves): pattern, synthesis, and theories. *Ethology, Ecology, and Evolution*, **17**, 363–449.
- Chapin, J. P. 1954. The calendar of Wideawake Fair. *Auk*, **71**, 1–15.
- Chapin, J. P. & Wing, L. W. 1959. The Wideawake calendar, 1953–58. *Auk*, **76**, 153–158.
- Chastel, O., Lacroix, A. & Kersten, M. 2003. Pre-breeding energy requirements: thyroid hormone, metabolism and the timing of reproduction in house sparrows *Passer domesticus*. *Journal of Avian Biology*, **34**, 298–306.
- Chernetsov, N., Berthold, P. & Querner, U. 2004. Migratory orientation of first-year white storks (*Ciconia ciconia*): inherited information and social interactions. *Journal of Experimental Biology*, **207**, 937–943.
- Cockburn, A. 1998. Evolution of helping behavior in cooperatively breeding birds. *Annual Reviews in Ecology and Systematics*, **29**, 141–177.
- Conner, J. K. & Hartl, D. L. 2004. *A Primer of Ecological Genetics*. Sunderland, Massachusetts: Sinauer.
- Conradt, L. & Roper, T. J. 2003. Group decision-making in animals. *Nature*, **421**, 155–158.
- Conradt, L. & Roper, T. J. 2005. Consensus decision making in animals. *Trends in Ecology and Evolution*, **20**, 449–456.
- Couzin, I., Krause, J., Franks, N. & Levin, S. 2005. Effective leadership and decision-making in animal groups on the move. *Nature*, **433**, 513–516.
- Croxall, J. P. 1991. Constraints on reproduction in albatrosses. *Acta XX Congressus Internationalis Ornithologici*, **1**, 281–302.
- Cutts, C. J. & Speakman, J. R. 1994. Energy savings in formation flight of pink-footed geese. *Journal of Experimental Biology*, **189**, 251–261.
- Dall, S., Giraldeau, L.-A., Olsson, O., McNamara, J. & Stephens, D. 2005. Information and its use by animals in evolutionary theory. *Trends in Ecology and Evolution*, **20**, 187–193.
- Danchin, E. & Wagner, R. 1997. The evolution of coloniality: the emergence of new perspectives. *Trends in Ecology and Evolution*, **12**, 342–347.
- Danchin, E., Giraldeau, L.-A., Valone, T. J. & Wagner, R. H. 2004. Public information: from nosy neighbors to cultural evolution. *Science*, **305**, 487–491.
- Davidson, A. & Menaker, M. 2003. Birds of a feather clock together sometimes: social synchronization of circadian rhythms. *Current Opinion in Neurobiology*, **13**, 765–769.
- Davies, C., Fischer, H. & Gwinner, E. 1969. Die Brutzeiten einiger Gänsearten und ihrer Bastarde in identischen Bedingungen. *Oecologia*, **3**, 266–276.
- Davies, N. B. 2000. *Cuckoos, Cowbirds and Other Cheats*. London: T. & A. D. Poyser.
- Davis, L. 1988. Coordination of incubation routines and mate choice in Adélie penguins (*Pygoscelis adeliae*). *Auk*, **105**, 428–432.
- Dawson, A., Hinsley, S., Ferns, P., Bonser, R. & Eccleston, L. 2000. Rate of moult affects feather quality: a mechanism linking current reproductive effort to future survival. *Proceedings of the Royal Society of London, Series B*, **267**, 2093–2098.
- DeCoursey, P. 2004. The behavioral ecology and evolution of timing systems. In: *Chronobiology: Biological Timekeeping* (Ed. by J. C. Dunlap, J. Loros & P. DeCoursey), pp. 27–65. Sunderland, Massachusetts: Sinauer.
- Delhey, K., Johnsen, A., Peters, A., Andersson, S. & Kempnaers, B. 2003. Paternity analysis reveals opposing selection pressures on crown coloration in the blue tit (*Parus caeruleus*). *Proceedings of the Royal Society of London, Series B*, **270**, 2057–2063.
- Del Negro, C., Kreutzer, M. & Gahr, M. 2000. Sexually stimulating signals of canary (*Serinus canaria*) songs: evidence for a female-specific auditory representation in the HVC nucleus during the breeding season. *Behavioural Neuroscience*, **114**, 526–542.
- Dhondt, A. 1973. Postjuvenile and postnuptial moult in a Belgian population of great tits *Parus major* with some data on captive birds. *Gerfaut*, **63**, 187–209.
- Dingle, H. 1996. *Migration: the Biology of Life on the Move*. Oxford: Oxford University Press.
- Doligez, B., Cadet, C., Danchin, E. & Boulinier, T. 2003. When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. *Animal Behaviour*, **66**, 973–988.
- Drent, R. & Daan, S. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea*, **68**, 225–252.
- Drent, R., Both, C., Green, M., Madsen, J. & Piersma, T. 2003. Pay-offs and penalties of competing migratory schedules. *Oikos*, **103**, 274–292.
- Düttmann, H., Dieleman, S. & Groothuis, T. 1999. Timing of moult in male and female shelducks *Tadorna tadorna*: effects of androgens and mates. *Ardea*, **87**, 33–39.
- Dunlap, J. C., Loros, J. & DeCoursey, P. (Eds) 2004. *Chronobiology: Biological Timekeeping*. Sunderland, Massachusetts: Sinauer.
- Dunn, M., Copelson, M. & Workman, L. 2004. Trade-offs and seasonal variation in territorial defence and predator evasion in the European robin *Erithacus rubecula*. *Ibis*, **146**, 77–84.
- Ens, B., Choudhury, S. & Black, J. M. 1996. Mate fidelity and divorce in monogamous birds. In: *Partnerships in Birds: the Study of Monogamy* (Ed. by J. M. Black), pp. 344–402. Oxford: Oxford University Press.
- Ezaki, Y. 1988. Mate desertion by male great reed warblers *Acrocephalus arundinaceus* at the end of the breeding season. *Ibis*, **130**, 427–437.
- Farner, D. & Gwinner, E. 1980. Photoperiodicity, circannual and reproductive cycles. In: *Avian Endocrinology* (Ed. by A. Epplé & M. Stetson), pp. 331–366. New York: Academic Press.
- Figuerola, J. & Jovani, R. 2001. Ecological correlates in the evolution of moult strategies in Western Palearctic passerines. *Evolutionary Ecology*, **15**, 183–192.
- Forslund, P. & Larsson, K. 1995. Intraspecific nest parasitism in the barnacle goose: behavioural tactics of parasites and hosts. *Animal Behaviour*, **50**, 509–517.
- Forsman, J. T., Seppänen, J.-T. & Mönkkönen, M. 2002. Positive fitness consequences of interspecific interaction with a potential competitor. *Proceedings of the Royal Society of London, Series B*, **269**, 1619–1623.

- Forstmeier, W., Kuijper, D. & Leisler, B. 2001. Polygyny in the dusky warbler, *Phylloscopus fuscatus*: the importance of female qualities. *Animal Behaviour*, **62**, 1097–1108.
- Fraser Darling, F. F. 1938. *Bird Flocks and the Breeding Cycle*. London: Cambridge University Press.
- Fraser Darling, F. F. 1952. Social behaviour and survival. *Auk*, **69**, 183–191.
- Freeberg, T. M. 1998. The cultural transmission of courtship patterns in cowbirds, *Molothrus ater*. *Animal Behaviour*, **56**, 1063–1073.
- Galef, B. 2004. Approaches to the study of traditional behaviors in free-living animals. *Learning and Behavior*, **32**, 53–61.
- Galef, B. & Heyes, C. M. (Eds) 2004. Social learning and imitation. Special Issue of *Learning and Behaviour*, **32**, 1–140.
- Gauthreaux, S. 1978. The ecological significance of behavioral dominance. In: *Perspectives in Ethology*. Vol. 3: *Social Behavior* (Ed. by P. P. Bateson & P. R. Klopfer), pp. 17–54. New York: Plenum.
- Gil, D. & Gahr, M. 2002. The honesty of bird song: multiple constraints for multiple traits. *Trends in Ecology and Evolution*, **17**, 133–141.
- Giraldeau, L.-A., Valone, T. J. & Templeton, J. J. 2002. Potential disadvantages of using socially acquired information. *Philosophical Transactions: Biological Sciences*, **357**, 1559–1566.
- Goldmann, B., Gwinner, E., Karsch, F., Saunders, D., Zucker, I. & Ball, G. 2004. Circannual rhythms and photoperiodism. In: *Chronobiology: Biological Timekeeping* (Ed. by J. C. Dunlap, J. Loros & P. DeCoursey), pp. 107–142. Sunderland, Massachusetts: Sinauer.
- González-Solís, J. 2004. Regulation of incubation shifts near hatching by giant petrels: a timed mechanism, embryonic signalling of food availability? *Animal Behaviour*, **67**, 663–671.
- Gorissen, L. & Eens, M. 2004. Interactive communication between male and female great tits (*Parus major*) during the dawn chorus. *Auk*, **121**, 184–191.
- Goymann, W. & Wingfield, J. C. 2004a. Allostatic load, social stress and stress hormones: the costs of social status matter. *Animal Behaviour*, **67**, 591–602.
- Goymann, W. & Wingfield, J. C. 2004b. Competing females and caring males: sex steroids in African black coucals, *Centropus grillii*. *Animal Behaviour*, **68**, 733–740.
- Greenberg, R. & Salewski, V. 2005. Ecological correlates of wintering social systems in New World and Old World migratory passerines. In: *Birds of Two Worlds: the Ecology and Evolution of Migration* (Ed. by R. Greenberg & P. Marra), pp. 336–358. Baltimore, Maryland: Johns Hopkins University Press.
- Grieco, F., van Noordwijk, A. J. & Visser, M. E. 2002. Evidence for the effect of learning on timing of reproduction in blue tits. *Science*, **296**, 136–138.
- Griffith, S. C., Owens, I. P. F. & Thuman, K. A. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Molecular Ecology*, **11**, 2195–2212.
- Gunnarsson, T. G., Gill, J. A., Sigurbjörnsson, T. & Sutherland, W. J. 2004. Arrival synchrony in migratory birds. *Nature*, **431**, 646.
- Gwinner, E. 1975. Die circannuale Periodik der Fortpflanzungsaktivität beim Star (*Sturnus vulgaris*) unter dem Einfluß gleich- und andersgeschlechtiger Artgenossen. *Zeitschrift für Tierpsychologie*, **38**, 34–43.
- Gwinner, E. 1986. *Circannual Rhythms: Endogenous Annual Clocks in the Organization of Seasonal Processes*. Berlin: Springer.
- Gwinner, E. 1996. Circannual clocks in avian reproduction and migration. *Ibis*, **138**, 47–63.
- Gwinner, E. 1999. Rigid and flexible adjustments to a periodic environment: role of circadian and circannual programs. In: *Proceedings of the 22nd International Ornithological Congress* (Ed. by N. Adams & R. Slotow), pp. 2366–2378. Johannesburg: BirdLife South Africa.
- Gwinner, E. & Helm, B. 2003. Circannual and circadian contributions to the timing of avian migration. In: *Avian Migration* (Ed. by P. Berthold, E. Gwinner & E. Sonnenschein), pp. 81–95. Berlin: Springer.
- Gwinner, E., König, S. & Zeman, M. 1995. Endogenous gonadal, LH and moult rhythms in tropical stonechats: effect of pair bond on period, amplitude, and pattern of circannual cycles. *Journal of Comparative Physiology A*, **177**, 73–79.
- Gwinner, H., van't Hof, T. & Zeman, M. 2002. Hormonal and behavioural responses of starlings during a confrontation with males or females at nest boxes during the reproductive season. *Hormones and Behavior*, **42**, 21–31.
- Hagelin, J., Jones, I. & Rasmusen, L. 2003. A tangerine-scented social odour in a monogamous seabird. *Proceedings of the Royal Society of London, Series B*, **270**, 1323–1329.
- Hahn, B. & Silverman, E. In press. Social cues facilitate habitat selection: American redstarts establish breeding territories in response to song. *Biology Letters*.
- Hahn, T., Swingle, J., Wingfield, J. & Ramenofsky, M. 1992. Adjustments of the prebasic molt schedule in birds. *Ornis Scandinavia*, **23**, 314–321.
- Hahn, T., Boswell, T., Wingfield, J. & Ball, G. 1997. Temporal flexibility in avian reproduction: patterns and mechanisms. In: *Current Ornithology*. Vol. 14 (Ed. by V. Nolan, Jr & E. Ketterson), pp. 39–80. New York: Plenum.
- Hall, M. 2004. A review of hypotheses for the functions of avian duetting. *Behavioral Ecology and Sociobiology*, **55**, 415–430.
- Hamilton, W. J. 1967. Social aspects of bird orientation mechanisms. In: *Animal Orientation and Navigation* (Ed. by R. M. Storm), pp. 51–71. Corvallis: Oregon State University Press.
- Hau, M., Wikelski, M. & Wingfield, J. P. 1998. A neotropical forest bird can measure the slight changes in tropical photoperiod. *Proceedings of the Royal Society of London, Series B*, **265**, 89–95.
- Helm, B. & Gwinner, E. 1999. Timing of postjuvenile molt in African (*Saxicola torquata axillaris*) and European (*Saxicola torquata rubicola*) stonechats: effects of genetic and environmental factors. *Auk*, **116**, 589–603.
- Helm, B. & Gwinner, E. 2001. Nestling growth and post-juvenile molt under a tight seasonal schedule in stonechats *Saxicola torquata maura* from Kazakhstan. *Avian Science*, **1**, 31–42.
- Helm, B., Gwinner, E. & Trost, L. 2005. Flexible seasonal timing and migratory behavior: results from stonechat breeding programs. In: *Bird Hormones and Bird Migrations: Analyzing Hormones in Droppings and Egg Yolks and Assessing Adaptations in Long-distance Migration* (Ed. by U. Bauchinger, W. Goymann & S. Jenni-Eiermann), pp. 216–227. New York: New York Academy of Sciences.
- Helms, C. 1963. The annual cycle and Zugunruhe in birds. *Proceedings of the International Ornithological Congress*, **13**, 925–939.
- Hemborg, C. & Lundberg, A. 1998. Costs of overlapping reproduction and moult in passerine birds: an experiment with the pied flycatcher. *Behavioral Ecology and Sociobiology*, **43**, 19–23.
- Hemborg, C. & Merilä, J. 1998. A sexual conflict in collared flycatchers, *Ficedula albicollis*: early male moult reduces female fitness. *Proceedings of the Royal Society of London, Series B*, **265**, 2003–2007.
- Hiebert, S., Ramenofsky, M., Salvante, K., Wingfield, J. C. & Gass, C. 2000. Noninvasive methods for measuring and manipulating corticosterone in hummingbirds. *General and Comparative Endocrinology*, **120**, 235–247.
- Hill, G. E. 2002. *A Red Bird in a Brown Bag. The Function and Evolution of Colourful Plumages in the House Finch*. Oxford: Oxford University Press.

- Höglund, J. & Alatalo, R. V. 1995. *Leks*. Princeton, New Jersey: Princeton University Press.
- Holberton, R. 1993. An endogenous basis for differential migration in the dark-eyed junco. *Condor*, **95**, 580–587.
- Houston, A. & McNamara, J. 1999. *Models of Adaptive Behaviour: an Approach Based on State*. Cambridge: Cambridge University Press.
- Hughes, L. 2000. Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution*, **15**, 56–61.
- Hyman, J. 2005. Seasonal variation in response to neighbours and strangers by a territorial songbird. *Ethology*, **111**, 951–961.
- Immelmann, K. 1971. Ecological aspects of periodic reproduction. In: *Avian Biology*. Vol. 1 (Ed. by D. S. Farner & J. R. King), pp. 341–389. New York: Academic Press.
- Ims, R. A. 1990. The ecology and evolution of reproductive synchrony. *Trends in Ecology and Evolution*, **5**, 135–140.
- James, P. 1956. Destruction of warblers on Padre island, Texas, in May, 1951. *Wilson Bulletin*, **68**, 224–227.
- Jehl, J. 1990. Aspects of the molt migration. In: *Bird Migration: Physiology and Ecophysiology* (Ed. by E. Gwinner), pp. 102–113. Berlin: Springer.
- Jehl, J., Henry, A. E. & Ellis, H. I. 2003. Optimizing migration in a reluctant and inefficient flier: the eared grebe. In: *Avian Migration* (Ed. by P. Berthold, E. Gwinner & E. Sonnenschein), pp. 199–209. Berlin: Springer.
- van der Jeugd, H. P. 2001. Large barnacle goose males can overcome the social costs of natal dispersal. *Behavioral Ecology*, **12**, 275–282.
- van der Jeugd, H. P. & Blaakmeer, K. 2001. Teenage love: the importance of trial liaisons, subadult plumage and early pairing in barnacle geese. *Animal Behaviour*, **62**, 1075–1083.
- van der Jeugd, H. P. & McCleery, R. 2002. Effects of spatial autocorrelation, natal philopatry, and phenotypic plasticity on the heritability of laying date. *Journal of Evolutionary Biology*, **15**, 380–387.
- van der Jeugd, H. P., van der Veen, I. T. & Larsson, K. 2002. Kin clustering in barnacle geese: familiarity or phenotype matching? *Behavioral Ecology*, **13**, 786–790.
- Jenni, L. & Winkler, R. 1994. *Moult and Ageing of European Passerines*. London: Academic Press.
- Kalela, O. 1954. Über den Revierbesitz bei Vögeln und Säugetieren als populationsökologischer Faktor. *Annals of the Zoological Society of Vanamo*, **16**, 1–48.
- Kempnaers, B. 1993. The use of a breeding synchrony index. *Ornis Scandinavica*, **24**, 84.
- Kempnaers, B. 1995. Polygyny in the blue tit: intra- and intersexual conflicts. *Animal Behaviour*, **49**, 1047–1064.
- Ketterson, E. & Nolan, V., Jr. 1983. The evolution of differential bird migration. In: *Current Ornithology*. Vol. 1 (Ed. by R. F. Johnson), pp. 357–402. New York: Plenum.
- Ketterson, E., Nolan, V., Jr., Casto, J., Buerkle, C., Clotfelter, E., Grindstaff, J., Jones, K., Lipar, J., McNabb, F., Neudorf, D., Parker-Renga, I., Schoech, S. & Snajdr, E. 2001. Testosterone, phenotype and fitness: a research program in evolutionary behavioral ecology. In: *Avian Endocrinology* (Ed. by A. Dawson & C. Chaturvedi), pp. 19–40. New Delhi: Narosa.
- König, S., Gwinner, E. & Helm, B. 2002. Programmed patterns of territorial aggression in first-year European and African stonechats (*Saxicola torquata rubicola* and *S. t. axillaris*). *Ecology of Birds*, **24**, 579–594.
- Komdeur, J., Richardson, D. & Burke, T. 2004. Experimental evidence that kin discrimination in the Seychelles warbler is based on association and not on genetic relatedness. *Proceedings of the Royal Society of London, Series B*, **271**, 963–969.
- Krebs, J. & Davies, N. B. 1987. *An Introduction to Behavioural Ecology*. Oxford: Blackwell.
- Kruuk, L. E. B. 2004. Estimating genetic parameters in wild populations using the 'animal model'. *Philosophical Transactions of the Royal Society of London, Series B*, **359**, 873–890.
- Lack, D. 1943–1944. The problem of partial migration. *British Birds*, **37**, 122–130, 143–150.
- Lack, D. 1950. The breeding seasons of European birds. *Ibis*, **92**, 288–316.
- Lack, D. 1968. *Ecological Adaptations for Breeding in Birds*. London: Methuen.
- Laland, K. 2004. Social learning strategies. *Learning and Behaviour*, **32**, 4–14.
- Lambrechts, M. M., Perret, P. & Blondel, J. 1996. Adaptive differences in the timing of egg laying between different populations of birds result from variation in photoresponsiveness. *Proceedings of the Royal Society of London, Series B*, **263**, 19–22.
- Landys-Ciannelli, M. M., Ramenofsky, M., Piersma, T., Jukema, J., Castricum Ringing Group & Wingfield, J. C. 2002. Baseline and stress-induced plasma corticosterone during long-distance migration in the bar-tailed godwit, *Limosa lapponica*. *Physiological and Biochemical Zoology*, **75**, 101–110.
- Larsson, K. 1996. Genetic and environmental effects on the timing of wing moult in the barnacle goose. *Heredity*, **76**, 100–107.
- Lea, R., Georgiou, G. & Sharp, P. J. 1997. Neural activation at the onset of incubation. In: *Perspectives in Avian Endocrinology* (Ed. by S. Harvey & R. Etches), pp. 257–266. Bristol: Journal of Endocrinology Press.
- Lehrmann, D. 1964. Control of behaviour cycles in reproduction. In: *Social Behavior and Organization among Vertebrates* (Ed. by W. Etkin), pp. 143–166. Chicago: University of Chicago Press.
- Leitner, S., van't Hof, T. & Gahr, M. 2003. Flexible reproduction in wild canaries is independent of photoperiod. *General and Comparative Endocrinology*, **130**, 102–108.
- Lewis, R. A. & Orcutt, F. S. 1971. Social behaviour and avian sexual cycles. *Scientia* (Rivista di Scienza, Milano, Italy), **5/6**, 1–24.
- Lissaman, P. B. S. & Shollenberger, C. A. 1970. Formation flight of birds. *Science*, **168**, 1003–1005.
- Loonen, M. J. 1997. Goose breeding ecology: overcoming successive hurdles to raise goslings. Ph.D thesis, University of Groningen.
- Lorenz, K. 1935. Der Kumpan in der Umwelt des Vogels. *Journal für Ornithologie*, **83**, 137–215, 289–413.
- Lyon, B. E. 2003. Ecological and social constraints on conspecific brood parasitism by nesting female American coots (*Fulica americana*). *Journal of Animal Ecology*, **72**, 47–60.
- McGraw, K. & Hill, G. 2004. Mate attentiveness, seasonal timing, of breeding, and long-term pair bonding in the house finch (*Carpodacus mexicanus*). *Behaviour*, **141**, 1–13.
- Maney, D., Schoech, S. & Wingfield, J. C. 1999. Environmental endocrinology and the timing of reproduction: interaction of photoperiod and temperature. In: *Proceedings of the 22nd International Ornithological Congress* (Ed. by N. Adams & R. Slotow), pp. 279–294. Johannesburg: BirdLife South Africa.
- Marques, M. D. & Waterhouse, J. (Eds). 2004. *Rhythms and ecology: do chronobiologists still remember nature?* Special Issue of *Biological Rhythm Research*, **35**, 1–2.
- Merilä, J. & Sheldon, B. 2001. Avian quantitative genetics. In: *Current Ornithology*. Vol. 16 (Ed. by V. Nolan, Jr & E. Ketterson), pp. 179–255. New York: Plenum.
- Miller, A. H. 1962. Bimodal occurrence of breeding in an equatorial sparrow. *Proceedings of the National Academy of Sciences, U.S.A.*, **48**, 396–400.

- Mistlberger, R. & Skene, D. 2004. Social influences on mammalian circadian rhythms: animal and human studies. *Biological Reviews*, **79**, 533–556.
- Moore, F., Gauthreaux, S., Kerlinger, S. A. & Simons, T. R. 1995. Habitat requirements during the migration period: important link in conservation. In: *Ecology and Management of Neotropical Migrant Landbirds* (Ed. by T. E. Martin & D. M. Finch), pp. 121–144. New York: Oxford University Press.
- Moore, F., Mabey, S. & Woodrey, M. 2003. Priority access to food in migratory birds: age, sex and motivational asymmetries. In: *Avian Migration* (Ed. by P. Berthold, E. Gwinner & E. Sonnenschein), pp. 281–292. Berlin: Springer.
- Moore, M. C. 1982. Hormonal responses of free-living male white-crowned sparrows to experimental manipulation of female sexual behavior. *Hormones and Behavior*, **16**, 323–329.
- Morton, G. & Morton, M. 1990. Dynamics of postnuptial moult in free-living mountain white-crowned sparrows. *Condor*, **92**, 813–828.
- Mota, P. G. & Depraz, V. 2004. A test of the effect of male song on female nesting behaviour in the serin (*Serinus serinus*): a field playback experiment. *Ethology*, **110**, 841–850.
- Myers, J. P. 1981. A test of three hypotheses for latitudinal segregation of the sexes in wintering birds. *Canadian Journal of Zoology*, **59**, 1527–1534.
- Myers, J. P. 1983. Space, time and the pattern of individual association in a group-living species: sanderlings have no friends. *Behavioral Ecology and Sociobiology*, **12**, 129–134.
- Myers, J. P. 1984. Spacing behaviour of nonbreeding shorebirds. In: *Shorebirds: Migration and Foraging Behavior* (Ed. by J. Burger & B. L. Olla), pp. 271–321. New York: Plenum.
- Naguib, M., Amrhein, V. & Kunc, H. 2004. Effects of territorial intrusions on eavesdropping neighbors: communication networks in nightingales. *Behavioral Ecology*, **15**, 1011–1015.
- Nakagawa, S. & Waas, J. 2004. 'O sibling, where art thou?' A review of avian sibling recognition with respect to mammalian literature. *Biological Reviews*, **79**, 101–119.
- Naumann, J. F. 1897. *Naturgeschichte der Vögel Mitteleuropas*. Vols 1–12. Gera-Untermhaus: Fritz Eugen Koehler.
- Nelson, D. & Soha, J. 2004. Male and female white-crowned sparrows respond differently to geographic variation in song. *Behaviour*, **141**, 53–69.
- Newton, I. 1966. The moult of the bullfinch *Pyrrhula pyrrhula*. *Ibis*, **108**, 41–87.
- Newton, I. (Ed.) 1989. *Lifetime Reproduction in Birds*. London: Academic Press.
- Nilsson, J.-Å. 1999. Fitness consequences of timing of reproduction. In: *Proceedings of the 22nd International Ornithological Congress* (Ed. by N. Adams & R. Slotow), pp. 224–247. Johannesburg: Bird-Life South Africa.
- Nilsson, J.-Å. & Svensson, E. 1996. The cost of reproduction: a new link between current reproductive effort and future reproductive success. *Proceedings of the Royal Society of London, Series B*, **263**, 711–714.
- van Noordwijk, A. J. 1989. Reaction norms in genetical ecology. *BioScience*, **39**, 453–458.
- Norris, D. R., Marra, P., Kyser, T., Sherry, T. & Ratcliffe, L. 2004a. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society of London, Series B*, **271**, 59–64.
- Norris, D. R., Marra, P., Montgomerie, R., Kyser, T. & Ratcliffe, L. 2004b. Reproductive effort, molting latitude, and feather color in a migratory songbird. *Science*, **306**, 2249–2250.
- Öst, M., Ydenberg, R., Lindström, K. & Kilpi, M. 2003. Body condition and the grouping behaviour of brood-caring female common eiders (*Somateria mollissima*). *Behavioral Ecology and Sociobiology*, **54**, 451–457.
- Owen, M. & Ogilvie, M. A. 1979. Wing moult and weights of barnacle geese in Spitsbergen. *Condor*, **81**, 42–52.
- Pärt, T. & Doligez, B. 2003. Gathering public information for habitat selection: prospecting birds cue on parental activity. *Proceedings of the Royal Society of London, Series B*, **270**, 1809–1813.
- Peake, T. M. 2005. Eavesdropping in communication networks. In: *Animal Communication Networks* (Ed. by P. K. McGregor), pp. 13–37. Cambridge: Cambridge University Press.
- Perrins, C. 1970. The timing of birds' breeding seasons. *Ibis*, **112**, 242–255.
- Peters, A., Astheimer, L., Boland, C. & Cockburn, A. 2000. Testosterone is involved in acquisition and maintenance of sexually-selected male plumage in superb fairy-wrens, *Malurus cyaneus*. *Behavioral Ecology and Sociobiology*, **47**, 438–445.
- Petrie, M. & Kempenaers, B. 1998. Extra-pair paternity in birds: explaining variation between species and populations. *Trends in Ecology and Evolution*, **13**, 52–58.
- Petrie, M. & Williams, A. 1993. Peahens lay more eggs for peacocks with larger trains. *Proceedings of the Royal Society of London, Series B*, **251**, 127–131.
- Piersma, T. 1983. Communal roosting of black-tailed godwits *Limosa limosa* on the Mokkebank. *Limosa*, **56**, 1–8.
- Piersma, T. 1987. Population turnover in groups of wing-moulting waterbirds: the use of a natural marker in great crested grebes. *Wildfowl*, **38**, 37–45.
- Piersma, T. 1988. The annual moult cycle of great crested grebes. *Ardea*, **76**, 82–95.
- Piersma, T. 2002a. Energetic bottlenecks and other design constraints in avian annual cycles. *Integrated and Comparative Biology*, **42**, 51–67.
- Piersma, T. 2002b. When a year takes 18 months: evidence for a strong circannual clock in a shorebird. *Naturwissenschaften*, **89**, 278–279.
- Piersma, T. & Jukema, J. 1993. Red breasts as honest signals of migratory quality in a long-distance migrant, the bar-tailed godwit. *Condor*, **95**, 163–177.
- Piersma, T., Lindeboom, R. & van Eerden, M. R. 1988. Foraging rhythm of great crested grebes *Podiceps cristatus* adjusted to diel variations in the vertical distribution of their prey *Osmerus eperlanus* in a shallow eutrophic lake in The Netherlands. *Oecologia*, **76**, 481–486.
- Piersma, T., Zwarts, L. & Bruggemann, J. H. 1990. Behavioural aspects of the departure of waders before long-distance flights: flocking, vocalizations, flight paths and diurnal timing. *Ardea*, **78**, 157–184.
- Piersma, T., Hoekstra, R., Dekinga, A., Koolhaas, A., Wolf, P., Battley, P. F. & Wiersma, P. 1993. Scale and intensity of intertidal habitat use by knots *Calidris canutus* in the western Wadden Sea in relation to food, friends and foes. *Netherlands Journal of Sea Research*, **31**, 331–357.
- Piersma, T., Mendes, L., Hennekens, J., Ratiarison, S., Groenewold, S. & Jukema, J. 2001. Breeding plumage honestly signals likelihood of tapeworm infestation in females of a long-distance migrating shorebird, the bar-tailed godwit. *Zoology*, **104**, 41–48.
- Piertney, S. B., MacColl, A. D. C., Racey, P. A., Bacon, P. J., Lambin, X. & Dallas, J. F. 2000. Matrilineal genetic structure and female-mediated gene flow in red grouse (*Lagopus l. scoticus*): an analysis using mtDNA. *Evolution*, **54**, 279–289.
- Pigliucci, M. 2001. *Phenotypic Plasticity. Beyond Nature and Nurture*. Baltimore, Maryland: Johns Hopkins University Press.
- Pravosudov, V., Mendoza, S. & Clayton, N. 2003. The relationship between dominance, corticosterone, memory, and food caching

- in mountain chickadees (*Poecile gambeli*). *Hormones and Behavior*, **44**, 93–102.
- Pulido, F. & Berthold, P.** 2003. Quantitative genetic analysis of migratory behaviour. In: *Avian Migration* (Ed. by P. Berthold, E. Gwinner & E. Sonnenschein), pp. 53–77. Berlin: Springer.
- Rappole, J. H.** 1995. *Ecology of Migrant birds: a Neotropical Perspective*. Washington, D.C.: Smithsonian Institution Press.
- Rappole, J. H. & Warner, D. H.** 1976. Relationships between behaviour, physiology and weather in avian transients at a migration stopover site. *Oecologia*, **26**, 193–212.
- Raveling, D. G.** 1969. Preflight and flight behaviour of Canada geese. *Auk*, **86**, 671–681.
- Reed, M., Bouludier, T., Danchin, E. & Oring, L.** 1999. Informed dispersal: prospecting by birds for breeding sites. In: *Current Ornithology*. Vol. 15 (Ed. by V. Nolan, Jr, E. Ketterson & C. Thompson), pp. 189–259. New York: Kluwer.
- Rees, E.** 1987. Conflict of choice within individual pairs of Bewick's swans regarding their migratory movement to and from the wintering grounds. *Animal Behaviour*, **35**, 1685–1693.
- Rees, E.** 1989. Consistency in the timing of migration for individual Bewick's swans. *Animal Behaviour*, **38**, 384–393.
- Ricklefs, R. E.** 2004. The cognitive face of avian life histories. *Wilson Bulletin*, **116**, 119–133.
- Ricklefs, R. E. & Wikelski, M.** 2002. The physiology/life-history nexus. *Trends in Ecology and Evolution*, **17**, 462–468.
- Riebel, K.** 2003. The 'mute' sex revisited: vocal production and perception learning in female songbirds. *Advances in the Study of Behaviour*, **33**, 49–86.
- Rockwell, R. F. & Cooke, F.** 1977. Gene flow and local adaptation in a colonially nesting dimorphic bird: the lesser snow goose (*Anser caerulescens*). *American Naturalist*, **111**, 91–97.
- Rohwer, F. C. & Anderson, M. G.** 1988. Female-based philopatry, monogamy and the timing of pair formation in migratory waterfowl. In: *Current Ornithology*. Vol. 5 (Ed. by R. Johnston), pp. 187–221. New York: Kluwer.
- Rowan, W.** 1926. On photoperiodism, reproductive periodicity and the annual migrations of birds and certain fishes. *Proceedings of the Boston Society of Natural History*, **38**, 147–189.
- Runfeldt, S. & Wingfield, J.** 1985. Experimentally prolonged sexual activity in female sparrows delays termination of reproductive activity in their untreated mates. *Animal Behaviour*, **33**, 403–410.
- Sandberg, R.** 2003. Stored fat and the migratory orientation of birds. In: *Avian Migration* (Ed. by P. Berthold, E. Gwinner & E. Sonnenschein), pp. 515–526. Berlin: Springer.
- Schjorring, S.** 2001. Ecologically determined natal philopatry within a colony of great cormorants. *Behavioral Ecology*, **12**, 287–294.
- Schwabl, H. & Silverin, B.** 1990. Control of partial migration and autumnal behaviour. In: *Bird Migration: Physiology and Ecophysiology* (Ed. by E. Gwinner), pp. 144–155. Berlin: Springer.
- Sheldon, B. C., Kruuk, L. E. B. & Merila, J.** 2003. Natural selection and inheritance of breeding time and clutch size in the collared flycatcher. *Evolution*, **57**, 406–420.
- Siikamäki, P., Hovi, M. & Rätti, O.** 1994. A trade-off between current reproduction and moult in the pied flycatcher: an experiment. *Functional Ecology*, **8**, 587–593.
- Silverin, B., Massa, R. & Stokkan, K.** 1993. Photoperiodic adaptation to breeding at different latitudes in great tits. *General and Comparative Endocrinology*, **90**, 14–22.
- Simons, A.** 2004. Many wrongs: the advantage of group navigation. *Trends in Ecology and Evolution*, **19**, 553–555.
- Slagsvold, T.** 1999. Sexual conflict in birds with biparental care: share of care in small vs. large broods and late vs. early broods. In: *Proceedings of the 22nd International Ornithological Congress* (Ed. by N. Adams & R. Slotow), pp. 2622–2638. Johannesburg: BirdLife South Africa.
- Smith, H.** 2004. Selection for synchronous breeding in the European starling. *Oikos*, **105**, 301–311.
- Smith, V. A., King, A. P. & West, M.** 2000. A role of her own: female cowbird influences on vocal development. *Animal Behaviour*, **60**, 599–609.
- Starck, J. M. & Ricklefs, R. E. (Eds)** 1998. *Avian Growth and Development*. New York: Oxford University Press.
- Stevenson, I. & Bryant, D.** 2000. Climate change and constraints on breeding. *Nature*, **406**, 366–367.
- Stresemann, E. & Stresemann, V.** 1967. Inheritance of the adaptation in moult. *Proceedings of the International Ornithological Congress*, **14**, 75–80.
- Studds, C. E. & Marra, P.** 2005. Nonbreeding habitat occupancy and population processes: an upgrade experiment with a migratory bird. *Ecology*, **86**, 2380–2385.
- Sutherland, W. J.** 1998. Evidence for flexibility and constraint in migration systems. *Journal of Avian Biology*, **29**, 441–446.
- Tamm, S.** 1980. Bird orientation: single homing pigeons compared to small flocks. *Behavioral Ecology and Sociobiology*, **7**, 319–322.
- Terrill, S.** 1987. Social dominance and migratory restlessness in the dark-eyed junco (*Junco hyemalis*). *Behavioral Ecology and Sociobiology*, **21**, 1–11.
- Thomas, D., Blondel, J., Perret, P., Lambrechts, M. & Speakman, J.** 2001. Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. *Science*, **291**, 2598–2600.
- Thompson, C. W.** 1991. The sequence of molts and plumages in painted buntings and implications for theories of delayed plumage maturation. *Condor*, **93**, 209–235.
- Tinbergen, N.** 1953. *Social Behaviour in Animals*. London: Methuen.
- Tarmontin, A. D., Wingfield, J. C. & Brenowitz, E.** 1999. Contributions of social cues and photoperiod to seasonal plasticity in the adult avian song control system. *Journal of Neuroscience*, **19**, 476–483.
- Urquhart, E. D.** 2002. *Stonechats*. London: Christopher Helm.
- Valone, T. J.** 1989. Group foraging, public information, and patch estimation. *Oikos*, **56**, 357–363.
- Veen, J.** 1977. Functional and causal aspects of nest distribution in colonies of the sandwich tern (*Sterna s. sandvicensis* Lath.). *Behaviour, Supplement*, **20**, 1–193.
- Veen, T., Borge, T., Griffith, S., Saetre, G., Bures, S., Gustafsson, L. & Sheldon, B.** 2001. Hybridization and adaptive mate choice in flycatchers. *Nature*, **411**, 45–50.
- Visser, M. E. & Lambrechts, M. M.** 1999. Information constraints in the timing of reproduction in temperate zone birds: great and blue tits. In: *Proceedings of the 22nd International Ornithological Congress* (Ed. by N. Adams & R. Slotow), pp. 279–294. Johannesburg: BirdLife South Africa.
- Visser, M. E., van Noordwijk, A. J., Tinbergen, J. M. & Lessells, C. M.** 1998. Warmer springs lead to mis-timed reproduction in great tits (*Parus major*). *Proceedings of the Royal Society of London, Series B*, **265**, 1867–1870.
- Waas, J. R., Caulfield, M., Colgan, P. W. & Boag, P.** 2000. Colony sound facilitates sexual and agonistic activities in royal penguins. *Animal Behaviour*, **60**, 77–84.
- Waas, J. R., Colgan, P. W. & Boag, P.** 2005. Playback of colony sound alters the breeding schedule and clutch size in zebra finches (*Taeniopygia guttata*) colonies. *Proceedings of the Royal Society of London, Series B*, **272**, 383–388.
- Wachtmeister, C. A.** 2001. Display in monogamous pairs: a review of empirical data and evolutionary explanation. *Animal Behaviour*, **61**, 861–868.

- Wagner, R. & Danchin, E. 2003. Conspecific copying: a general mechanism of social aggregation. *Animal Behaviour*, **65**, 405–408.
- Wagner, R., Danchin, E., Bouludier, T. & Helfenstein, F. 2000. Colonies as byproducts of commodity selection. *Behavioral Ecology*, **11**, 572–573.
- Walther, G., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebe, T., Fromentin, J., Guldberg, O. & Bairlein, F. 2002. Ecological responses to recent climate change. *Nature*, **416**, 389–395.
- Wallraff, H. G. 1978. Social interrelations involved in migratory orientation of birds: possible contribution of field studies. *Oikos*, **30**, 401–404.
- Ward, S., Speakman, J. R. & Slater, P. J. B. 2003. The energy cost of song in the canary, *Serinus canaria*. *Animal Behaviour*, **66**, 893–902.
- Warnock, N. & Takekawa, J. 2003. Use of radio telemetry in studies of shorebirds: past contributions and future directions. *Wader Study Group Bulletin*, **100**, 138–150.
- West, M. J., King, A. P. & White, D. J. 2003. The case for developmental ecology. *Animal Behaviour*, **66**, 617–622.
- Whaling, C., Soha, J., Nelson, D., Lasley, B. & Marler, P. 1998. Photoperiod and tutor access affect the process of vocal learning. *Animal Behaviour*, **56**, 1075–1082.
- Whitfield, D. P. 2003. Raptor predation on non-breeding shorebirds: some thoughts for the future. *Wader Study Group Bulletin*, **100**, 134–137.
- Whitfield, D. P. & Brade, J. J. 1991. The breeding behaviour of the knot *Calidris canutus*. *Ibis*, **133**, 246–255.
- Wingfield, J. C. 1980. Fine temporal adjustment of reproductive functions. In: *Avian Endocrinology* (Ed. by A. Eppler & M. H. Stetson), pp. 367–389. London: Academic Press.
- Wingfield, J. C. & Farner, D. S. 1979. Some endocrine correlates of re-nesting after loss of clutch or brood in the white-crowned sparrow, *Zonotrichia leucophrys gambelii*. *General and Comparative Endocrinology*, **38**, 322–331.
- Wingfield, J. C. & Jacobs, J. 1999. The interplay of innate and experiential factors regulating the life history cycle of birds. In: *Proceedings of the 22nd International Ornithological Congress* (Ed. by N. Adams & R. Slotow), pp. 2417–2443. Johannesburg: BirdLife South Africa.
- Wingfield, J. C. & Marler, P. 1988. Endocrine basis of communication in reproduction and aggression. In: *The Physiology of Reproduction* (Ed. by E. Knobil & J. Neill), pp. 1647–1677. New York: Raven.
- Wingfield, J. C. & Monk, D. 1994. Behavioral and hormonal responses of male song sparrows to estradiol-treated females during the non-breeding season. *Hormones and Behavior*, **28**, 146–154.
- Wingfield, J. C. & Silverin, B. 2002. Ecophysiological studies of hormone-behaviour relations in birds. *Hormones, Brain and Behaviour*, **2**, 587–647.
- Wingfield, J. C., Hegner, R., Dufty, A. & Ball, G. 1990. The 'challenge hypothesis': theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *American Naturalist*, **136**, 829–846.
- Wingfield, J. C., Jacobs, J., Tramontin, A., Perfito, N., Meddle, S., Maney, D. & Soma, K. K. 2000. Toward an ecological basis of hormone-behavior interactions in reproduction of birds. In: *Reproduction in Context: Social and Environmental Influences on Reproductive Physiology and Behavior* (Ed. by K. Wallen & J. Schneider), pp. 86–128. Cambridge, Massachusetts: MIT Press.
- Wingfield, J. C., Soma, K. K., Wikelski, M., Meddle, S. L. & Hau, M. 2001. Life cycles, behavioural traits, and endocrine mechanisms. In: *Avian Endocrinology* (Ed. by A. Dawson & C. M. Chaturvedi), pp. 3–17. New Delhi: Narosa.
- Wu, G. & Giraldeau, L.-A. 2005. Risky decisions: a test of risk sensitivity in socially foraging flocks of *Lonchura punctulata*. *Behavioral Ecology*, **16**, 8–14.
- Zentall, T. 2004. Action imitation in birds. *Learning and Behaviour*, **32**, 15–23.